

THE QUARTERLY REVIEW
of BIOLOGY

VOLUME VI
1931

Published by
THE WILLIAMS & WILKINS COMPANY
BALTIMORE
U. S. A.

THE QUARTERLY REVIEW OF BIOLOGY

RAYMOND PEARL, *Editor*
The Johns Hopkins University

ASSISTED BY

R. W. HEGNER	BLANCHE F. POOLER	JOHN RICE MINER
<i>Contributing Editor</i>	<i>Assistant Editor</i>	<i>Assistant Editor</i>
CHARLES P. WINSOR		
<i>Assistant Editor in charge of New Biological Books</i>		
<i>The Johns Hopkins University</i>		

ADVISORY BOARD

ANATOMY.....	LEWIS H. WEED.....	<i>The Johns Hopkins University</i>
ANTHROPOLOGY.....	A. L. KROEBER.....	<i>University of California</i>
BEHAVIOR AND COMPAR-		
ATIVE PSYCHOLOGY....	K. S. LASHLEY.....	<i>Institute for Juvenile Research</i>
BOTANY.....	A. IRVING W. BAILEY.....	<i>Harvard University</i>
CYTOLOGY.....	EDMUND B. WILSON.....	<i>Columbia University</i>
ECOLOGY.....	WILLIAM MORTON WHEELER.....	<i>Harvard University</i>
EMBRYOLOGY.....	E. G. CONKLIN.....	<i>Princeton University</i>
EXPERIMENTAL		
MORPHOLOGY.....	ROSS G. HARRISON.....	<i>Yale University</i>
GENERAL PHYSIOLOGY	{ LAWRENCE J. HENDERSON.....	<i>Harvard University</i>
	{ G. H. PARKER.....	<i>Harvard University</i>
GENETICS.....	{ R. A. EMERSON.....	<i>Cornell University</i>
	{ T. H. MORGAN.....	<i>California Institute of Technology</i>
GEOGRAPHICAL DISTRI-		
BUTION AND TAXON-		
OMY.....	ALEXANDER G. RUTHVEN.....	<i>University of Michigan</i>
PALEONTOLOGY.....	JOHN C. MERRIAM.....	<i>Carnegie Institution</i>
RUSSIAN BIOLOGICAL		
LITERATURE.....	W. W. ALPATOV.....	<i>University of Moscow</i>
ZOOLOGY.....	FRANK R. LILLIE.....	<i>University of Chicago</i>

CONTENTS

No. 1, MARCH, 1931

	PAGE
The Problem of the Origin of Germ Cells.....	<i>Florence Heyes</i> 1
The Rôle of Bacteria in the Nutrition of Protozoa.....	<i>J. Murray Luck, Grace Sheets, and John O. Thomas</i> 46
Nerve Conduction in Relation to Nerve Structure.....	<i>R. W. Gerard</i> 59
Facts and Theories of Bird Flight.....	<i>Lucien H. Warner</i> 84
New Biological Books:	
Brief Notices.....	99

No. 2, JUNE, 1931

Analysis of Intersexuality in the Gipsy-Moth.....	<i>Richard Goldschmidt</i> 125
Biological Organization.....	<i>David L. Watson</i> 143
Death and Its Causes.....	<i>W. W. Lepeschkin</i> 167
The "Concept of Organism" and the Relation Between Embryology and Genetics.	
Part III.....	<i>J. H. Woodger</i> 178
The Present Status of the Problems of Orientation and Homing by Birds	
.....	<i>Lucien H. Warner</i> 208
Mitogenetic Rays.....	<i>Alexander Hollaender and Eugene Schoeffel</i> 215
New Biological Books:	
Brief Notices.....	223

No. 3, SEPTEMBER, 1931

The Biological Effects of Short Radiations.....	<i>Charles Packard</i> 253
Quantitative Relations in Biological Processes and the Radiation Hypothesis of	
Chemical Activation.....	<i>Charles D. Snyder</i> 281
Unisexual Progenies and Sex Determination in <i>Sciara</i>	<i>C. W. Metz</i> 306
Forms of Nitrogen Assimilated by Plants.....	<i>F. E. Allison</i> 313
The Vacuum Tube Oscillator in Biology	
.....	<i>G. Murray McKinley and John G. McKinley, Jr.</i> 322
The Problem of Color Vision in Fishes.....	<i>Lucien H. Warner</i> 329
New Biological Books:	
Brief Notices.....	349

No. 4, DECEMBER, 1931

The Primate Basis of Human Sexual Behavior.....	<i>Gerrit S. Miller, Jr.</i> 379
Haploidy in Metazoa.....	<i>Franz Schrader and Sally Hughes-Schrader</i> 411
Hibernation in Mammals.....	<i>George E. Johnson</i> 439
The Three Types of Mortality Curve.....	<i>István Szabó</i> 462
New Biological Books:	
Brief Notices.....	464
The Cost of Biological Books in 1931.....	<i>John R. Miner</i> 494
Index to Volume VI.....	497

THE QUARTERLY REVIEW of BIOLOGY



THE PROBLEM OF THE ORIGIN OF GERM CELLS

By FLORENCE HEYS

Department of Zoology, Washington University

SINCE the time when August Weismann (1834-1914) first made a clear distinction between the soma and the germ plasm, and introduced the now familiar idea of the uniqueness and continuity of germ cells, the origin and history of definitive germ cells have become subjects of active investigation. Many have tried their hands at it and arrived at varying conclusions.

Weismann ('83, '04) based his "*Descendenztheorie*" primarily upon his work on the Hydromedusae. In 1907 Goette in a study of Hydroids found no verification for the "germinal track" of Weismann. But the hypothesis of Weismannian continuity soon gained support from work on certain invertebrates, such as the parasitic round worm, *Ascaris* (Boveri, '92), and others, where it seemed that germ cells could be traced back definitely to early segmentation stages. According to this interpretation a part of the original fertilized egg is set apart as germ plasm early in cleavage, a single cell of the four-celled embryo, in the case of *Ascaris*.

Work on the history of vertebrate germ cells dates back to Waldeyer ('70), who first observed distinguishable germ cells in the germinal epithelium, from which

he supposed them to have been derived. MacLeod ('81) in the teleost, *Hippocampus*, and the needle fish (teleost), *Belone acus*, observed that the sex cells appear in the somatopleure and splanchnopleure rather late in development, and thought them to be differentiated peritoneal cells. He came to the conclusion that the genital fold originates in a group of cells on the surface of the epithelium.

Eigenmann in 1891 believed he could identify primordial germ cells in the late cleavage stages (thirty-two cell stage the earliest) of the teleost, *Micrometrus aggregatus*, but presumably no other investigator has been able to recognize germ cells in any vertebrate until after the germ layers are formed. Three years before Weismann published the *Origin of Sex Cells in the Hydromedusae*, Nussbaum ('80) had expressed the view that germ cells were segregated early in individual development and not derived from other (that is, somatic) cells, thus embodying the idea of continuity. Neither of these theories lacks supporters. Hoffman in 1886 and Dustin in 1907 confirmed Waldeyer's theory of origin from the germinal epithelium; Kuschakewitsch ('10) and Gatenby ('16) added experimental evi-

dence. Beard ('00), B. M. Allen ('06, '07, '10, '11), and Dodds ('10) upheld the early segregation theory of Nussbaum.

Waldeyer's observation of recognizably

primordial germ cells and following their migration in the developing embryo until they reached the site of the gonad.

Basing his conclusions upon work on

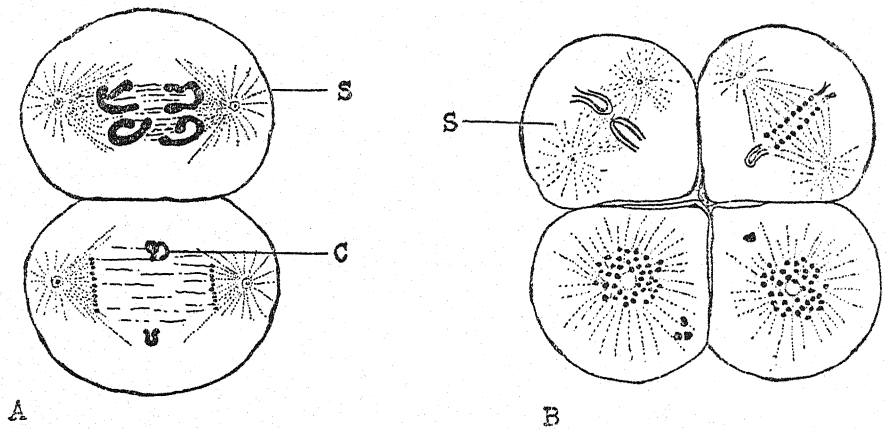


FIG. 1. EARLY CLEAVAGE OF THE EGG OF *ASCARIS*, SHOWING THE ORIGIN OF GERM CELLS

A—two-cell stage, the chromosomes of one cell remain intact, those in the other cell fragmented. B—division of four-cell stage showing three cells with fragmented chromosomes and the stem cell with chromosomes intact. S—stem cell from which the germ cells are derived. C—chromatin eliminated into the cytoplasm. Redrawn from Boveri.

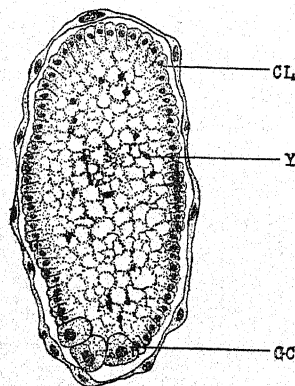


FIG. 2. DEVELOPMENT OF THE EGG OF THE FLY, *Mliastor americana*, SHOWING THE CLEAVAGE CELLS AT THE PERIPHERY AND THE GERM CELLS AT THE POSTERIOR END

CL—cleavage cells. GC—germ cells. Y—yolk. After Hegner in the *Journal of Morphology*.

different cells in the germinal epithelium, together with the evidence of other workers for early segregation, suggested the possibility of tracing the so-called

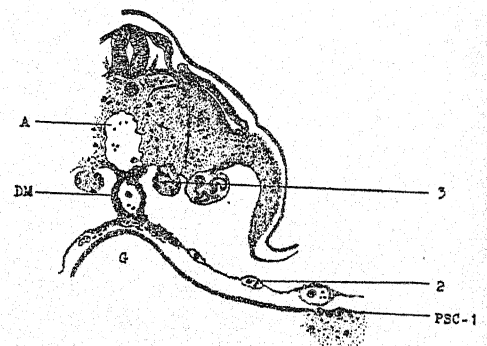


FIG. 3. SCHEMATIC SECTION THROUGH THE MIDBODY REGION OF A YOUNG EMBRYO ILLUSTRATING THE MANNER IN WHICH PRIMORDIAL GERM CELLS ARE BELIEVED TO ORIGINATE IN THE YOLK-SAC ENTODERM AND MIGRATE TO THE DEVELOPING GONAD

A—aorta. DM—dorsal mesentery. G—gut. PSC 1—primordial germ cells in the entoderm. PSC 2—primordial germ cells in the blood vessels. PSC 3—primordial germ cells at the site of the developing gonad. After Patten—*Embryology of the Chick*.

the mouse, Jenkinson in 1913 figured primordial germ cells and described them as forming the yolk sac and migrating to

the genital ridge. He was cautious, however, in expressing an opinion as to their ultimate fate, and admitted the possibility of peritoneal origin for some of the germ cells.

Child ('06) was convinced from work on the cestode, *Moniezia expansa*, that the germ cells develop from cells of the parenchymal syncytium, which must be regarded as composed of differentiated tissue cells. In connection with the development of his theory of differentiation ('15) he says:

In the tapeworm, *Moniezia*, for example, the sex cells arise from the parenchyma and apparently any parenchymal cells which lie within the region involved in the production of sex cells may undergo dedifferentiation and take part in the process. Even the large muscle cells may give rise to testes. . . . In such cases the muscle fibre undergoes degeneration, the vacuoles disappear, and the nucleus begins to divide. ('15, p. 331).

Fuss ('11, '13) upon the basis of Rubaschkin's ('08, '10) proposed method of differential staining of germ cells, located what he identified as "*extraregionare Geschlechtszellen*" in the intestinal epithelium of the four-weeks human embryo (quoted by Simkins, '28). The supposed sex cells were arranged in such a way as to suggest an active migration from the entoderm of the gut into the visceral peritoneum.

Felix ('12), who may or may not have been influenced by Rubaschkin's differential coloration method, distinguished two categories of germ cells in the course of gametogenesis. These he designated as primary and secondary genital cells. The primary genital cells, he contended, had a special origin from the segmentation cells, and were, therefore, extra-regional in origin, that is, they arose directly from the blastomeres of early cleavage and remained distinctly reproductive cells, destined to migrate into the developing gonad. But these cells, after so careful a

preservation, were found to degenerate and contribute nothing to the definitive germ-cell population. The secondary genital cells, Felix believed, were derived from the peritoneum of the gonads, and these passed through growth and maturation processes into ova or sperm, as the case might be. The two categories of cells had no physiological or genetic connection.

De Winiwarter and Sainmont ('09) from studies of germ cells of embryos and kittens, also maintained that the primordial germ cells in the cat all degenerate and are replaced by a proliferation from the germinal peritoneum. De Winiwarter later ('10) declared that a like fate could be demonstrated for primordial germ cells in man.

Thus it is admitted by many that the so-called primordial germ cells *do appear* in early embryonic stages, and, when first distinguishable, are in the gut entoderm. From there they migrate to the genital ridge, such cells being the pre-primordium of the gonad.

At the time of these relatively early investigations, the last word by no means had been said on the origin of the definitive procreation cells. Many cytological contributions have appeared in recent years, favoring continuity from generation to generation, and, by inference, at least, supporting the hypothesis that all germ cells now in existence go back in an unbroken line to the germinal materials of the first living thing upon the earth.

Others find evidence in favor of the view that a discontinuity of germ cells exists between the generations, each crop of definitive germ cells arising anew from the peritoneum of the gonads. The conclusions arrived at in these later investigations place their authors readily in four groups:

- I. Those who deny early segregation of germ cells, and believe that germ-cell formation is a matter of the differentiation of somatic cells.
- II. Those who admit early segregation of germ cells, but conclude that such cells are not definitive and degenerate, to be replaced by proliferations of new cells from the germinal epithelium.
- III. Those whose investigations have led to the conclusion that germ cells are segregated early and migrate to the site of the developing gonad. These persist as definitive germ cells, but their numbers are increased periodically by a proliferation from the epithelium.
- IV. Those who believe that the definitive germ cells are set aside at an early stage in embryonic development not to be replaced later by transformation of differentiated peritoneal cells. Their numbers are increased only by mitotic divisions.

GROUP I

From the standpoint of a study of cellular embryonic structure and of cell migration, this group of investigators fails to find in the history of germ cells, the continuity upon which adherents of the Weismannian hypothesis lay stress. They deny segregation entirely; primordial germ cells, as such, do not exist. Many of them consider the large cells so often observed by workers and called primordial sex cells, to be merely somatic cells in different phases of metabolic activity. It has been suggested that their enlargement is preparatory to cell division, or that they are cells which are enlarged because of being, for some reason, retarded in their division and which, therefore, have a longer resting (storage) period. The question of the formation of germ cells becomes thus purely a matter of differentiation of somatic cells.

The work of Hargitt

Of particular interest in this connection is the work of Hargitt ('13, '16, '17, '18, '19, '24, '25, '26), since it includes studies from both invertebrates and vertebrates.

The early work of Hargitt was on the origin of germ cells in Coelenterates. These results were presented in a series of papers from 1913 to 1919. From this work he concluded that germ cells are not segregated early in ontogeny and kept isolated until the time of maturity, but are differentiated at a time just preceding sexual maturity; and that they may arise directly from functional body cells.

The application of these results Hargitt considered rather far-reaching: namely, that the germ-plasm theory would have to be discarded, in so far, at least, as it related to the lower invertebrates, and it was suggested that eventually it might be discarded for the vertebrates as well. With his abandonment of the germ-plasm theory, the conclusion follows that there is fundamentally no distinction between germ cells and body cells.

After the publication of these results several writers on this and related subjects intimated that, while these conclusions might well apply to such simply-organized animals as the Coelenterates, they could hardly be referred to the highly-organized vertebrates. Hargitt, very possibly influenced by these suggestions, sought to extend his studies to the higher forms.

In 1924 Hargitt's paper appeared describing the origin of germ cells in the adult salamander, *Diemyctylus viridescens*. Here he suggested that the problem of the origin of germ cells in vertebrates might be divided into two phases. One is concerned with the earliest appearance and source of the primordial germ cells in ontogeny and their fate. The second phase deals with the relation of these to the germ cells of the adult which periodically produce the functional germ cells, as is true in those forms such as the salamander, where seasonal regeneration of the gonad seems to take place. Hargitt's

work on *Diemystylus* dealt only with this second phase.

The program followed was the critical examination of the tissues of the testis: the stroma, the young cysts containing spermatogonia and spermatocytes, the cysts containing spermatozoa, older degenerating cysts, interstitial cells, the germinal epithelium and peritoneum of the neighboring regions outside the testis. Hargitt considered that these categories include all possible sources of germ-cell origin in the adult.

In the stroma of the testis (connective

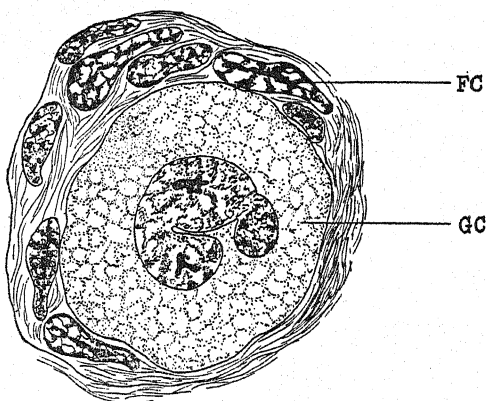


FIG. 4. GERM CELL WITH FOLLICLE CELL FORMING; BILOBED NUCLEUS CONSPICUOUS

FC—follicle cell. GC—germ cell. After Hargitt in *Jour. Morph.*

tissue) scattered, isolated cells were observed and identified as spermatogonia. Such cells were always found near the collecting ducts and in the stroma between the cysts. Hargitt identified these as germ cells by their size, differential staining behavior, and the fact that in some cases they were enclosed by a capsule of the stroma; but chiefly by the presence of a polymorphic nucleus, in this case bilobed. The presence of an attraction sphere was also used as an additional criterion of a germ cell.

Since these germ cells were found in the

stroma, it suggested to him that they are stroma cells differentiated into germ cells. Hargitt was of the opinion that their consistent, close association with adjacent collecting ducts is of the greatest significance. He did not consider for a moment that these were primordial, residual germ cells, but they must be a new generation of germ cells whose origin was the epithelial cells of the collecting ducts, since in all cases they were found in close proximity to the terminal branch of the duct. He observed mitosis going on in the peritoneum surrounding the testis and considered this a second source of the new generation of germ cells. But these cells from the epithelium migrate, after division, into the stroma and are later transformed into spermatogonia. In the process of differentiation, cells of the peritoneum seemed to take on first the typical polymorphic nucleus, which was considered the infallible sign of a germ cell in these tissues. These cells could be traced into the stroma. The appearance of the polymorphic nucleus was conspicuous and constituted the initial step in germ-cell transformation.

As a result of these studies in the salamander, their author concluded that what had been true for the Coelenterates was also true for the vertebrates, in so far, at least, as *Diemystylus* was concerned. If germ cells are early segregated, they must degenerate, for he found no trace of them in the adult. It, therefore, seemed logical to Hargitt to discard all previous views of the distinction between germ cells and body cells and the concept of germ-cell continuity.

Recently ('25, '26) two papers by Hargitt have completed the series. They carry the study into the mammals and treat of the first phase of the problem, that is, the earliest appearance and source

of primordial germ cells, if there be such, and the question of their ultimate destination. Hargitt indicates that a reliable answer to this question can come only from a careful study of the germ cells through the entire period of ontogeny, from their first appearance in the embryo until maturity. He undertook to make such a study in the albino rat. Using data given by Huber ('15) on the early development of the rat "1st day after insemination—ovum contains male and female pronuclei; 3rd day after insemination—four-celled stage of cleavage; 5th day—

these large cells: quoting Woods, "In the youngest embryo studied, in the blastoderm stage, practically all the cells, except those in the ectoderm, had all the characteristics of the primitive ova found in later embryos of from one to six millimeters." Hargitt says,

With such a universal distribution, it is hard to look upon them as germ cells, but this wide-spread diffusion would be entirely in accord with the view that they are merely enlarged local cells which have missed some cell division. . . . This would mean a lack of difference between germ cells and body cells, with a later differentiation of both from the embryonic tissues.

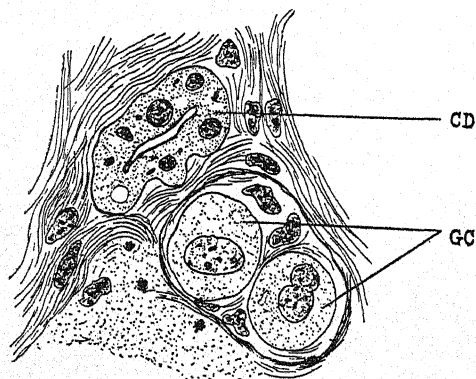


FIG. 5. A CYST CONTAINING TWO GERM CELLS SHOWN IN CLOSE PROXIMITY TO THE COLLECTING DUCT

CD—collecting duct. GC—germ cell. After Hargitt in *Jour. Morph.*

early blastodermic vesicle; etc.", Hargitt selected for study stages beginning with the primitive streak stage (9th day), a search being made for what might prove to be primordial germ cells.

Large cells of different staining reaction were found in the epithelial mesoderm, but these were also present in the ectoderm, the endoderm of the gut, and even in the extra-embryonic tissues. There was no distinction between these larger cells, wherever found. Hargitt points out that other workers, especially Woods ('02), observed a wide distribution of

Hargitt found evidence of the formation of the genital ridge from the peritoneal layer, an enlargement of cells in this layer, and a wandering of these cells into the genital-ridge region, similar to the periodic migration of cells from the germinal epithelium into the stroma of the testis which he observed in *Diemyctylus*. In these tissues the nuclei were spherical, large, and darkly-staining. As development progressed, from the thickening of the genital ridge until the twelfth or thirteenth days, when the gonad is truly distinguishable, the large cells in other regions, ectoderm, extra-embryonic membranes, entoderm and mesenchyme, disappeared, while the proportion of darkly-staining cells with plump, spherical nuclei increased in the genital ridge and nearby peritoneum. Only very rarely were large cells found between the kidney, aorta, genital ridge, and the gut. Hargitt explained the disappearance of these cells in the following way: all the retarded cells (large cells) which were observed earlier and had so wide a distribution are now, in the twelfth and thirteenth-day embryos, actively dividing, and the only large cells left are those differentiating from the peritoneum—the

germ cells. At this time only a clumping together of the large cells within the genital ridge was apparent, an observation which Hargitt considered of great importance.

In the earlier work, on *Diemictylus*, Hargitt had used the appearance of the polymorphic nucleus as the criterion of a germ cell, but from these studies he concluded that there is no single distinguishing characteristic or group of characteristics; the only satisfactory method, he says, is to trace the germ cells back step by step. In the rat such a procedure led him to the conclusion that there is no segregation of germ cells and no migration through a "germ track" into the gonad.

Hargitt's most recent paper ('26) reports the results of his work on the male rat, from the fourteenth day in embryonic development to maturity. After the fourteenth day the testis differentiated from the indifferent gonad by the separation of a definite surface layer, from which the sex cords arise. These cords were found to increase and grow by the activity of their own cells and not by further contributions from the germinal epithelium. The remainder of the history of the testis was purely a question of gradual differentiation. (Since the writing of this review Hargitt has extended his studies to the female rat with identical conclusions ('29).)

As a result of his studies on germ-cell origin and history, Hargitt is willing to discard entirely the concept of continuity: "Personally, I believe biology would be greatly the gainer by dropping the germ-plasm idea entirely and permanently." ('26, p. 290).

The Work of Firket

Firket ('14, '20) is of the opinion that the cytological aspect of mitochondria, used by some workers, particularly Rub-

aschkin ('10, '12) and Tschaschin ('10), is an unreliable criterion of germ cells, but finds it a convenient method for following these cells in their development. He concluded that in the chick most of the primary germ cells both of the ovary and testis eventually degenerated, and that the majority of definitive ova or spermatozoa were derived from the epithelial organs of the sex glands. Since these constituted a second generation of germ cells, they were called secondary germ cells. Nevertheless, Firket saw no reason why "certain of the primary germ cells might not produce some of the definitive cells, since it was impossible to distinguish between primary and secondary cells." ('20, p. 311).

In contrast to what he described in the chick, Firket found, in a study of the testis of young rats, that the two generations of germ cells could be distinguished from each other very easily, because the cells of the second generation, called secondary cells, arose only when those of the first generation, the primary cells, had entirely disappeared. Primary germ cells in the chick developed at least until the growth period, reaching well-characterized stages of preparation for maturation divisions. But in the rat he found no evidence that primary cells ever reached the period of growth, all apparently degenerating at an earlier stage.

The bearing of sex-reversal on the origin of germ cells

Studies on sex-reversal have been considered by some an important source of evidence in favor of the origin of definitive germ cells from the epithelium. Essenberg ('23, '26) in work on sex-reversal in the teleost, *Xiphophorus helleri*, reported germ-cell formation from the epithelium of the "ovarian cavity" after degeneration

of the ovary. Whatever the cause of this degeneration its occurrence has been demonstrated experimentally. The large oocytes disintegrated first, followed shortly by the medium cells, and finally by the very young oocytes, located close to the epithelium. The epithelial covering of the ovary completely disintegrated, but the epithelium of the so-called "ovarian cavity" was not subject to the disintegration process. After a period of rest, this epithelium again became active and proliferated germ cells which formed, by means of sex cords and later seminiferous tubules, a gonad of the opposite sex. Essenberg arrived at the conclusion that definitive germ cells in the teleost are not linear descendants of primordial germ cells, but originate from the peritoneum, and that the new gonad of the transforming fish arises from a part of this peritoneum: "It is interesting to note that the epithelium of the ovarian cavity which gives rise to the definitive male cells originates . . . from the peritoneum of the body cavity." ('26, p. 101).

Similar results were obtained in the fowl by Fell ('23), who studied gonads of eight birds representing various stages in sex-reversal from female to male. This author also found germ cells of the opposite sex proliferating from the peritoneal epithelium of the degenerating ovary. Cells from the sex cords gave rise later to seminiferous tubules, and finally to functional sperm.

No explanation is offered by either of these authors for the phenomenon of sex-reversal. Essenberg suggests that the factors must "reside in the gonad and possibly in the germ cells themselves." Until more is known of the causative factors in sex-reversal, the source of the cells which go to make up the transformed gonad remains a question.

The work of Simkins and others

Work by Simkins in 1923 on the mouse substantiated Hargitt, though Simkins was a little more ready to admit the possibility of germ-cell continuity than Hargitt. Simkins states that there is no segregation of germ cells and that none of the so-called primordial germ cells of early embryos migrates or has anything to do with the formation of the gonad. The large cells, so frequently seen, are not germ cells at all, but very active cells participating in the formation of other organs. Germ cells come only from the coelomic epithelium as it produces the genital thickening.

Kohno ('25) working on the "*Keimbahn*" of man recognized what he considered germ cells in the lateral plates of mesoderm of a 2.3-millimeter embryo, and as these plates were folded under the gut in 2.8-millimeter embryos, the germ cells moved up into the epithelium of the gut and mesentery, from which they migrated farther into the developing gonads in embryos measuring five to seven millimeters. But Simkins suggests the possibility that Kohno's "*Urogenitalzellen*" are somatic cells in different phases of activity or perhaps artifacts due to staining.

On the basis of his work on the mouse Simkins hesitates to discard the concept of continuity, but in a later paper ('28) on the origin of sex cells in man, he indicates his confidence in the conclusion that no strict independence of somatic and germ cells is demonstrable. Cytological examinations were made of human embryos of both sexes, measuring from 2.6 millimeters to twenty-five millimeters, when the gonad is definitely formed. Simkins considers the supposed germ cells to be liquified areas, surrounding a mitotic or degenerating nucleus, which have taken stain. He believes that the definitive

cells of both ovary and testis come from the smaller cells of the gonad, whose origin is from the peritoneum, and thus are transformed somatic cells. The suggestion is made that if the original germinal peritoneum is removed, no more cells will be produced, but if the gonad can be removed without the peritoneum then why not germ cells replaced by transformed soma cells? This suggestion indicates the relation of regeneration of gonads to the problem of germ-cell continuity, a study of which, as will be evident later, throws some light on the problem of continuity.

Very recently ('29) Wolf has concluded from studies of *Platypocilus maculatus* that the epithelial cells of the lining of the ovarian cavity transform into germ cells.

GROUP II

A second group of investigators includes those who observe the large, primordial germ cells and admit early segregation, but find no evidence of their persistence and therefore conclude that such cells are not definitive and degenerate to be replaced by proliferations of new cells from the germinal epithelium.

Perhaps the first to come to this conclusion was Mihalkovics, who in 1885, after a study of *Amniotes*, stated that prominent, early-appearing cells, which might be taken for germ cells, degenerate or disappear by division into smaller cells. These were different, he said, from the real primordial germ cells, which appeared later, and should not be confused with them. And Minot in 1894 expressed doubt that such cells had any relation to the genital region or could be looked upon as primordial germ cells, since they were correlated with cell division and disappeared long before germ cells were differentiated.

Von Berenberg-Gossler in work on birds

('12) and later ('14) on reptiles reported recognizable germ cells differentiating from the genital anlage coincident with its development. He believed that any large cells appearing before the gonads developed were not germ cells but participants in a late formation of mesenchyme. Von Berenberg-Gossler demonstrated the unreliability of the criterion proposed by Rubaschkin ('10, '12) and Tschaschin ('10) that a specific type of mitochondria is characteristic of germ cells.

Kingsbury ('13, '14) contended that in the cat proliferations of germ cells from the peritoneum take place up to thirty-three days post-partum, and that by this time most of the cells have passed through meiotic phases. He found no such proliferation just before the advent of sexual maturity, nor any periodic activity of the epithelium. The first proliferation, up to thirty-three days after birth, according to Kingsbury, gives rise to the definitive oocytes.

Kingery ('17) distinguished two separate formations of germ cells from the epithelial covering of the ovary in the white mouse. The oocytes of the embryonic proliferation remain for some time in the germinal peritoneum in a resting condition. These cells pass through phases of meiosis into a second resting stage before sinking into the stroma of the ovary and taking part in follicle formation. At birth the process has become retarded, and meiotic stages are to be found only in the epithelium itself. Kingery reported a second proliferation of cells beginning at three to four days before birth and continuing until thirty to forty-five days after birth.

According to Kingery's interpretation the true oocytes are of this second proliferation in contra-distinction to the cells of the first proliferation, all of which degenerate. He claims to have traced the

definitive germ cells from their inception in the germinal epithelium until they were ready for maturation, and up to the time when graafian follicles developed. Kingery takes issue in this report with de Winiwarter and Sainmont, and some others, who make meiotic phases the criterion of a true germ cell. The ultimate destination of a cell, he says, is the only reliable criterion, and when the ovary attains maturity, the germinal potentiality of the peritoneal cells is lost.

The work of Butcher

Butcher ('27) has made a study of the white rat with a view to determining whether ova are formed after birth and during sexual maturity from the epithelial covering of the ovary. Examination was made of the ovary and tissue immediately surrounding it at intervals from birth until adult life; and meiotic phases were observed up to the third day after birth. Soon, however, particularly the third and fourth days, a condition of degeneration was seen, affecting first the cytoplasm of the cells, the nucleus merging into a resting stage. A possible explanation for this regressive process, Butcher thinks, was the crowded condition of the ovary at this stage and the consequent inadequate blood supply. This process of degeneration was especially evident about the seventeenth day, when large cavities were seen in the follicles. Butcher believes that these germ cells which are so prominent at birth disappear long before the advent of maturity and that none ever persists to become a definitive ovum.

About the sixth to seventh days, while the degeneration process was progressing among the older germ cells, he observed certain small cells of the epithelial covering begin to enlarge. Quite frequently two such cells were seen to enlarge side by side as if they were daughter cells of

one small cell through mitosis. The nuclei, which formerly had been oval, began to enlarge and become spherical in form; the chromatin clumped together and stained more intensely. These young oocytes, for such they were considered, took on a spherical shape and gradually became pushed into the tunica, as definitive germ cells.

Butcher finds definite evidence that "a continuous proliferation and formation of germ cells goes on until about sixty-five days after birth, when the process becomes slightly retarded." Ovulation, of course, occurs before this time, since large corpora lutea are found. Contrary to the opinion of Kingery, Butcher believes that the germinal potentiality of the peritoneum is not lost at puberty:

... in fact, at some stages during post-pubertal life the process of the formation of germ cells is very marked. It would seem that such a condition must exist, since evidence, as interpreted by the writer, is steadily increasing that all follicles are relatively short-lived, and it is now considered by some untenable to conceive of eggs lasting the life-time of the individual ('27, p. 20).

The formation of germ cells from the epithelial covering of the ovary, according to Butcher, continues to take place until fecundity is lost at old age. A notable increase in mitotic activity in the epithelium was evident during oestrus. Cells enlarging in the epithelium were usually more common as the oestrous period approached than they were immediately following. The cells, likewise, seemed to lie deeper in the cortex as time progressed after each oestrous period. Butcher came to the conclusion that "... the process of germ-cell formation in the rat from the germinal epithelium, therefore, seems to be a continuous process throughout life."

A later ('28) study of germ-cell origin extended these conclusions to the lake

lamprey, *Petromyzon marinus unicolor*, with the exception that in this species the potentiality of the epithelium seemed to be lost gradually after the formation of the gonad, as no continuous proliferation process could be detected in the adult.

McCosh ('28) made studies of a series of ontogenetic stages in *Amblystoma maculatum* from cleavage until metamorphosis. Primordial germ cells, first located in the lateral mesoderm, were traced to a definitive position in the genital anlagen. Comparative counts of these cells in younger and more advanced stages gave evidence that few ever reach the site of the developing generative gland. McCosh believes that a few of these may survive, but that the majority of the procreation cells are of somatic origin. She describes the transformation of "small cuboidal or spindle-shaped cells with oval nuclei into large germ cells with immense polymorphic or lobate nuclei," an observation in agreement with that of Hargitt ('24) in *Diemyctylus*. These cells were abundant in all older individuals. "Successive stages in the evolution of a somatic cell into a reproductive cell" involve "an increase in size, changes in shape, and a new distribution of chromatin material."

GROUP III

A third group includes papers supporting the conclusion that germ cells are set apart early, migrate to the site of the developing ovary or testis and *persist*, their numbers being increased periodically by a proliferation from the epithelium.

Bohi ('04), who worked on the trout and the salmon, came to the conclusion that some of the germ cells are set apart early in development while others arise from the epithelial cells after the genital ridge is formed. He believed that the changing of epithelial cells into genital cells lasted for a brief period only, for in

embryos of 277 days or more, no transition cells were found. The number of germ cells was counted at different stages: from four to six in embryos of twenty-five days to twenty to fifty-four at 185 days after fertilization, at which the number remained fairly constant. After the 185 day mark was past a very rapid increase was observed (373 at 199 days), and was attributed to the transformation of peritoneal cells into germ cells. Bohi believed that the coelomic cells gave rise to indifferent cells, follicle cells, and germ cells; the cells on the sides of the genital fold gradually becoming transformed into germ cells.

Arai ('20) was perhaps the first to suggest continuous proliferation. In a statistical study of the post-partum history of the ovary in the rat, investigating particularly the number of ova at various ages, Arai states that the process of proliferation of new ova is most marked during the period from fifteen to sixty days, and may continue for a year after birth, although it proceeds at a much slower rate after maturity is attained. The degenerative process, which is constantly going on in the ovary, involving both primitive and definitive ova, is compensated by a continuous proliferation from the epithelium. The new cells grow, sink into the tunica albuginea and finally into the underlying stroma.

Allen ('22, '23) from careful studies of the oestrous cycle of the white mouse was led to the conclusion that at each normal oestrous period, young ova are added to the cortex of the adult ovary. He described them as arising from dividing cells in the germinal epithelium. If the angle of the cell undergoing mitosis to the surface of the ovary was more than thirty degrees, the proximal of the two daughter cells was considered to be cut off from the germinal epithelium and soon surrounded by a ring of adjacent epithelial cells.

Butcher, however, in 1927, found no verification of the observation that cells cut off with their long axes perpendicular to the surface necessarily become oocytes.

Cowperthwaite ('25), whose work will be discussed in Group IV, takes issue with Allen for lack of comparison between the appearance of the chromatin in young ova arising by proliferation of the germinal epithelium, and that in ova found before puberty. Cowperthwaite considered the meiotic phenomena of great importance, but Allen apparently observed none and deemed their absence a matter of no significance.

When mitosis was at its height, a statistical study of the proportion of very young oocytes in the cortex to slightly older ones led Allen to the belief that the cell divisions of the germinal peritoneum formed the germ cells but not the somatic tissue or stroma of the ovary. He found that there is present in the adult ovary shortly after each oestrous period a greater number of young oocytes than are observable after the dioestrous interval.

According to Allen the germ-cell population is added to periodically: "A cyclical proliferation of the germinal epithelium gives rise to a new addition of young ova to the cortex of the adult ovary at each normal oestrous period" ('23, p. 467). Allen's conclusions are thus contrary to those of Kingery that the germinal potentiality of the peritoneal cells is lost as the ovary attains maturity.

After studying a large number of ovaries from guinea pigs of various ages, including embryos and adults, Papanicolaou ('25) stated that there is a continuous process of oogenesis from the time of gonadal differentiation in the embryo up to the time of the cessation of sexual activity in the older females. The process gradually decreased with the increasing age of the individual. Papanicolaou observed, how-

ever, that at certain periods, especially during sexual maturity, a very marked activity of the epithelium was evident, resulting in the proliferation of many cells. This unusual periodicity he attributed to various "nutritive and hyperemic conditions" at these particular times.

The conclusions of Papanicolaou are in agreement with those of Butcher in so far as they subscribe to a continuous process of oögenesis.

In investigating the morphogenesis of the indifferent gonad and of the ovary, Brambell ('27) observed the usual large cells which have come to be called primordial germ cells. These were present in the primordium of the germinal ridge before the onset of epithelial proliferation, and were found in the mesentery of the gut and in the mesenchyme, near the germinal ridge, as well as in the germinal ridge, until the gonad had become "constricted off" from the surrounding peritoneum. Contrary to the experience of many, Brambell found no signs of degeneration. These early cells appeared to persist and to undergo maturation phases, and there was a marked absence of such cells from other parts of the embryo. But beside these Brambell found germ cells forming from the epithelial cells of the genital ridge:

Every intermediate stage between the undoubted germ cells and the undifferentiated germinal epithelial cells can be seen in a single section. The cytological evidence for the formation of the "primordial" germ cells in the germinal ridge is, therefore, satisfactory.

Furthermore, even if it were established that the primordial germ cells migrate into the germinal ridge from elsewhere,

and Brambell's own work brought some evidence that such was the case,

it would still be impossible to deny that others in every way indistinguishable from them were differentiated from the epithelial cells. It would be difficult to imagine a sufficient number of germ cells

migrating to account for the rapid increase in the number found in the gonad between the tenth and twelfth days, although many of those in the gonads are in mitosis ('27, p. 403-404).

GROUP IV

There is a fourth group of writers who uphold early segregation of germ cells as well as a strict independence of germ cells and somatic cells. These are the true adherents to the principle of Weismannian continuity who believe that the germ cells are set aside at an early stage in embryonic development, not to be duplicated or replaced later by transformed peritoneal cells. In this group belong investigations which have led to the conclusion that the sole source of definitive sex cells is the primordial germ cells, appearing in early segmentation stages. These cells, first recognizable, as a rule, in the gut endoderm migrate to the site of the gonad, where they increase in number by cell division only (see Fig. 3).

In a preliminary study of *Phrynosoma cornutum* (the horned toad), Jarvis ('08) traced the path of normal migration of germ cells from the entoblast of the vascular area of the blastoderm to the yolk stalk, intestine and sclerotome of the mesentery, and thence to the germinal anlagen. Many germ cells "lose their way" along this path. These "lost cells" thus come to lie in various parts of the embryo and soon degenerate. In general the conclusions of Jarvis substantiate Beard ('00). She states that the possibility that these degenerating cells in various regions of the embryo might be transitional forms between soma and germ cells seems precluded by the fact that they were never found in what she termed the path of normal migration, and especially by their absence from the germinal anlagen.

King, also in 1908, located early germ cells in the entoderm of the Anuran, *Bufo*

lentiginosus, and believed that the definitive germ cells arose only from primordial cells segregated early in development, but that peritoneal cells gave rise to all other elements of the sex gland. According to King, cyst formation takes place, but the cells of a cyst do not necessarily divide simultaneously. The cysts showed no evidence of fragmentation as has been observed by other writers on Anuran germ cells. King was led to the conclusion that in the female all the cells of a given cyst were descendants of a single, primary oogonium.

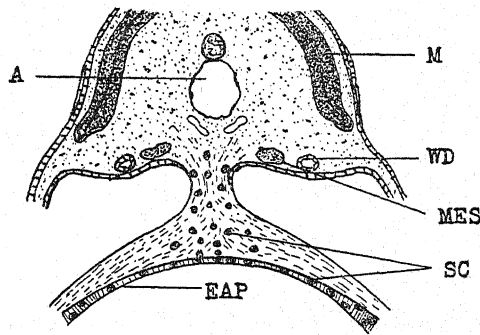


FIG. 6. DIAGRAMMATIC REPRESENTATION OF THE PATH OF GERM-CELL MIGRATION IN THE TURTLE, *CHRYSEMYS MARGINATA*

A—aorta. M—myotome. EAP—entoderm of the area pellucida. WD—Wolffian duct. MES—mesonephros. SC—sex cells. After Hegner in *The Germ-Cell Cycle in Animals*.

The work of Hegner

According to Hegner ('14) in his book on the germ-cell cycle of animals, germinal-epithelium theories of germ-cell origin have little evidence in their favor, since no one has "actually observed a transformation of peritoneal or mesoblast cells into germ cells." "On the other hand there is an abundance of proof that these cells (primordial germ cells) migrate from some distance into the position of the sex glands." ('14, p. 99).

Hegner's own work on Chrysomelid beetles ('09a) brought evidence of a migra-

tory process. In these insects the primordial germ cells were segregated at the posterior end of the egg at the time when the blastoderm was formed. The blastoderm was never completed beneath them, but a canal which formed in this region persisted, and through this at a later embryonic stage the germ cells migrated by means of amoeboid movements:

As soon as the germ cells of *Calligrapha* have passed through the pole-cell canal, they lose their pronounced, pseudopodia-like processes and become nearly spherical; nevertheless they (still) undergo a decided change in position. They move away from

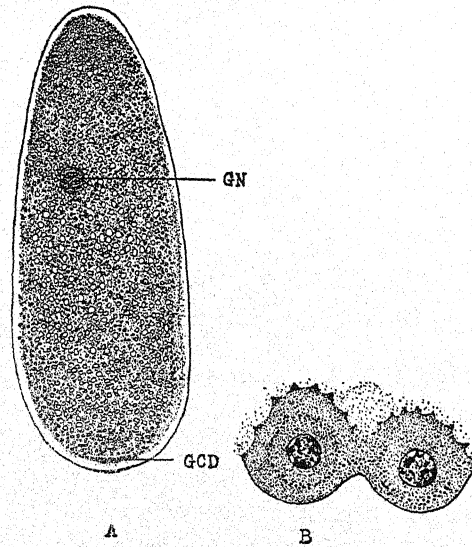


FIG. 7. A—LONGITUDINAL SECTION THROUGH THE EGG OF *CALLIGRAPHA BIGSBYANA* FOUR HOURS AFTER DEPOSITION, SHOWING GERM-CELL DISC AT THE POLE OF THE EGG. B—TWO TYPICAL GERM CELLS

GCD—germ-cell disc. GN—germ nuclei fusing. After Hegner in *The Germ-Cell Cycle in Animals*.

the inner end of the pole-cell canal, and creep along between the yolk and the germ-band. Thus two groups are formed near the developing coelomic sacs; each group probably contains an equal number of cells. . . . From this stage on, the germ cells are not very active; they move closer to one another to form the compact germ glands. I was unable to determine whether the later movements of the germ cells were due to an active migration or to the tension created by the growth of the surrounding tissues; the latter seems more probable ('09a, p. 280).

In paedogenetic reproduction in the fly, *Miastor americana*, Hegner ('12) followed the history of the germ cells from one generation to the next:—in the division from four to eight cells three of the four nuclei of the four-cell stage divide by mitosis in the usual manner, but one cell in division gives to its daughter cells only one half the usual chromatin. One of these reduced chromatin cells is always found at the end of the blastula in the pole-plasm. The single primordial germ cell divides three times giving eight germ cells. A resting period sets in, and these cells are passively carried to a point near the tail fold of the embryo. The eight oögonia separate into two groups of four each, and the ovary forms around them. Such a history looks like Weismannian continuity of germ-plasm. (See Fig. 2).

The work of Swift

Three papers by Swift, appearing in consecutive years ('14, '15, '16), described his researches on the germ cells of the chick. The first noticeable attributes of primordial germ cells recorded by Swift were their size and shape, both being conspicuously different from those of surrounding cells. The germ-cell nuclei were also definitely characteristic, but the most important criterion, according to Swift, was the large, ever-present attraction sphere. Rubaschkin ('08) and von Berenberg-Gossler ('12) stressed this criterion earlier. Swift gave little attention to mitochondrial elements, since he considered them not at all characteristic and quite like the mitochondria of somatic cells. According to him the germ cells arise in a region anterior and antero-lateral to the embryo at the margin of the area pellucida. Owing to the late appearance of mesoderm in this region, these cells were seen first between the entoderm and the ectoderm. They seemed to possess a migratory power of their own and entered

the mesoderm and later the blood vessels. Swift believes the primordial germ cells of his observation identical with the "entodermal wander-cells" described by Dantschakoff ('08), but he disagrees with her in that he observed no degeneration, which she believed eliminated all primordial germ cells so that they took no part whatsoever in gonad formation. Swift concluded from his observations that practically all primordial germ cells do persist, and are carried in the blood stream

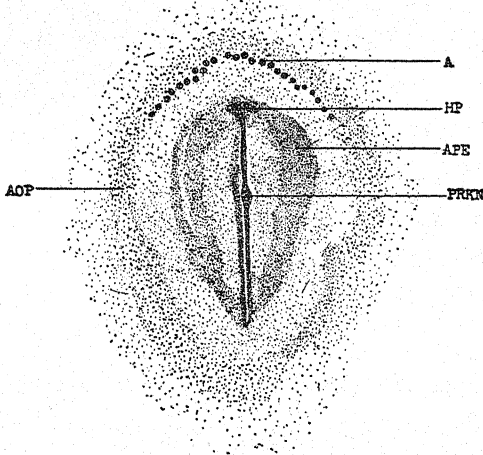


FIG. 8. SURFACE VIEW OF A PRIMITIVE-STREAK STAGE OF A CHICK EMBRYO, VIEWED BY TRANSMITTED LIGHT, SHOWING THE POINT AT WHICH THE PRIMORDIAL GERM CELLS ARISE

A—region at which the primordial germ cells arise. HP—head process. PRKN—primitive knot. AOP—area opaca. APE—area pellucida. After Swift in *Amer. Jour. Anat.*

to all parts of the embryo and vascular area. (Compare Fig. 3.) This general distribution maintains until the embryo has reached the stage of about twenty somites. From the twenty-second to the twenty-ninth-somite stages these cells gradually take up their residence in the splanchnic mesoderm and the coelomic epithelium. When the gonad proper begins to be formed about the sixth or seventh day of incubation, they pass into that organ, the extra-germinal tissues

arising as proliferated cords from the epithelium.

The work of Vanneman on the armadillo

In 1917 Vanneman, studying the armadillo, *Tatusia novemcincta*, was able to distinguish germ cells, and experienced no difficulty in identifying them from the earliest stages. Size and form were remarkably constant throughout development. The primordial germ cell is described by her as large, about twice the size of an ordinary erythrocyte, and, in contrast to neighboring cells, light in staining reaction. These cells were typically spherical, but at times, and especially in early stages, the shape was very suggestive of amoeboid movement. The cell outline was always very definite, and this was taken as one of the most dependable criteria of germ cells. Concerning the criteria used by other investigators for distinguishing germ cells, Vanneman has little to say except that neither was the presence of yolk substance sufficiently constant to be used in the identification nor the attraction sphere of Swift frequently enough apparent to be used as a criterion.

In the armadillo, as worked out by Patterson ('13), the usual cleavage stages take place with the formation of a typical mammalian blastocyst, consisting of one trophoblastic layer and an inner cell-mass of embryonic cells. A process of differentiation sets in through the migration of the entodermal mother-cells from among the ectodermal cells. These cells directly, or after division, migrate to the under surface of the cell-mass and presently become transformed into a continuous layer which splits from the ectoderm. The embryonic ectoderm now rounds up into a spherical mass which withdraws from the trophoblast, and pushes into the vesicle cavity, becoming included in a

layer of entoderm. Through the process of vacuolization, the ectoderm sphere now becomes a vesicle. After this stage the primary buds first appear from the thickened areas which have arisen on the opposite sides of the ectodermic vesicle through a shifting of cells. The primary buds show no signs of embryonic primordia, but each directly gives rise to two secondary diverticula, forming four buds which are soon extended, and begin to show the beginnings of four primitive streaks destined to become the quadruplets. Each embryo derives its ectoderm from a part of the lateral plate, while the entoderm arises from the primitive entodermal sac. From such a developmental beginning Vanneman considered it possible that the germ cells of all four embryos might have a common origin.

Early germ cells were located by Vanneman between the ectoderm and entoderm at the time when the primary buds and the ectodermic vesicle were in the process of formation. They were exceedingly few in number, a fact also recorded by Swift ('14) for the chick in embryos earlier than the primitive-streak stage. The cytological resemblance of these early cells to adjacent entodermal cells, together with the presence of cells actively dividing, suggested the possibility that at this point for the first time germ cells were being proliferated from segregated cells, which up to this time had not been distinguished from surrounding tissues. But it was not until the secondary bud-stage was reached that the germ cells were found in any numbers. Vanneman indicates that such an origin for germ cells is, in general, similar to Swift's findings as regards place, method, and time:

The entoderm of the mammalian blastocyst is analogous to the yolk sac entoderm of the lower vertebrates. It is not unreasonable to suppose that in the armadillo the germ cells arise during the

secondary bud state in the embryonic areas through the influence of the ectodermic vesicle upon the blastocyst-entoderm at the point where the two layers come into contact. Observation seems to confirm this. That the germ cells have not arisen in numbers any earlier may be due to the fact that there exists previous to the early primitive streak stages no incident, such as the coming in contact of ectodermic and entodermic layers, to favor the proliferation of germ cells. ('17, p. 335).

At the time when the embryo had attained four millimeters length and acquired a pronounced cervical bend, the germ cells were amoeboid in shape and were seen in the act of leaving the ventral interstitial wall to enter the surrounding mesenchyme tissue. In five to six millimeter embryos they appeared at the base of the well-developed mesentery, though usually not below the level of the three blood vessels of that region. They were also present in the loose mesenchyme below the aorta, en route to the germinal epithelium. In the ten millimeter embryo they were established in the indifferent gonad, slightly enlarged as if preparatory to division.

It was Vanneman's first idea that the germ cells of the four embryos of one vesicle might have a common origin as the early development suggested, but no evidence supporting such an origin was found, at least in the sense of having arisen from "a pre-localized region of the early blastocyst."

In the catfish, *Aminurus nebulosus*, Bachman ('14) traced the migration of germ cells beginning with embryos measuring 3.2 millimeters. Germ cells were distinct from all other cells at the 3.2-millimeter stage and thereafter. At this time they were present in the lateral plate of the mesoderm, from which they finally found their way to the germ-gland anlagen. Bachman reported no transformation of peritoneal cells and considered division the sole means of germ-cell multiplication.

Jordon ('17) favors early segregation and persistence of germ cells, and takes issue with von Berenberg-Gossler ('12, '14), who studied large cells in the ectoderm and mesoderm outside the genital region of reptiles and birds, and denied their germinal character, explaining them as participants in mesenchyme formation. Jordon says that such results are "unique and do not seem capable of being brought into harmony with results in any other form thus far studied—", and again, "this interpretation is more or less plausible but cannot be said to be wholly satisfactory."

From an extensive investigation of the germ-cell history in the brook lamprey, *Entosphenus wilderi* (Gage) Okkelberg ('21) was led to the belief that definitive germ cells take their origin from no other source than the primordial germ cells, and that the germ cells take no part in the formation of somatic structures. He distinguished germ cells by their size, structure, and location, and like Richards and Thompson ('21) considered migration passive, the shift in position of germ cells being accredited to a shifting of the tissues surrounding the cells. These cells were first identified in the brook lamprey when the mesoderm separated from the entoderm, before the germ layers were definitely established. During the early period of their history the germ cells were observed to shift from a lateral position in the mesoderm to a median position. No division of germ cells took place until the larvae were about 20 mm. in length. By this time the large germ cells had lost the yolk granules which characterized them earlier. After each mitotic division the two daughter cells separated slightly but remained in close proximity, forming cell nests. Peritoneal cells migrated into these nests and formed follicle cells. As sex differentiation approached the nests of cells gradu-

ally became constricted off, forming a definite germ gland.

The work of Swingle

Swingle ('21, '26) distinguished primordial germ cells in the entoderm of the bullfrog embryo, and traced them to the formation of the sex gland, and up to the time of metamorphosis. He located the earliest recognizable germ cells as a median ridge of yolk-laden cells just dorsal to the roof of the archenteron, ventral to the aorta, and separating the two mesodermal plates from each other. In embryos of eight millimeters length the germ-cell

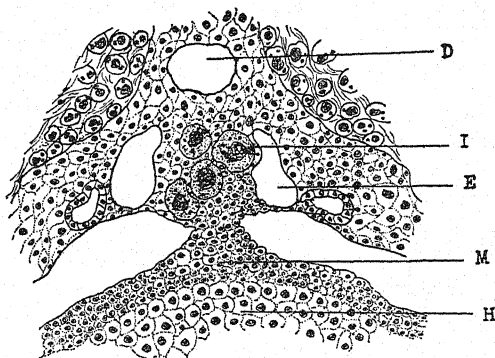


FIG. 9. TRANSVERSE SECTION THROUGH THE GERM-CELL REGION OF AN EIGHT-MILLIMETER LARVA

I—germ cells. M—mesentery. D—aorta. H—entoderm cells. E—cardinal veins. After Swingle in *Jour. Exper. Zool.*

ridge had become separated from the underlying entoderm forming the roof of the archenteron. Swingle believes that migration is by movement of surrounding tissues but also that there is an active migration of the germinal elements themselves. As development progressed this median ridge split longitudinally, and the cells of the two halves moved laterally on either side to form two independent ridges invested with peritoneum. At this stage the total embryo length was about nine millimeters. The two germinal

ridges next projected into the coelomic cavity and enlarged markedly, the number of cells being increased by cell division. When the tadpole had attained a length of thirty millimeters, the gonads were definitely formed, appearing as hollow sacs surrounded by a single layer of peritoneum and made up of one or two layers of germ cells.

All increase in the number of germ cells up to the forty millimeter length was, beyond question, Swingle thinks, by mitotic activity of the pre-existing (primordial) sexual elements. At the 40 mm. stage the germ cells seemed to enter a maturation process and passed through all the normal phases up to the first maturation division. In the act of division these spermatocytes disintegrated, and a resorption process set in. With the exception of a very few, all these cells degenerated. The few remaining cells persisted unchanged, and shortly before metamorphosis became very active, giving rise to a second generation of sexual elements.

At this time the gonads became filled with small cells which from their size, nuclear appearance, staining reaction, etc., seemed intermediate between mesothelial cells and true germ cells. The later history of these cells showed them to be germ cells, and the author considered them small germ-cell descendants of the primordial sexual elements, but he hesitates to deny the possibility of their origin from the peritoneum.

Swingle is inclined to agree with Hegner ('14) regarding the germ track in vertebrates, but he is not ready to believe that germinal-epithelium theories have so little in their favor. He says:

Though regarding himself as an entodermist, and taking the point of view that the "*Keimbahn*" is probably continuous in vertebrates and that there is no actual transformation of mesothelial elements into

sex cells, the writer admits that conditions are such in the bullfrog that it is impossible to state positively that the primordial germ cells of the bullfrog tadpole do give rise to the definitive sex cells of the adult frog. ('21, p. 289-290).

In this connection Swingle points out that the only adequate method of attack is by experimental procedure. Morphological methods are insufficient to determine whether or not a germ cell is a transformed epithelial element or a small descendant of the primordial line.

The work of Richards and Thompson

A paper by Richards and Thompson ('21) had as its special aim the definite identification of the primordial sex cells and the determination of the germinal path in *Fundulus* embryos. These authors experienced no difficulty in recognizing primordial germ cells, for they found them to maintain distinctive characteristics throughout the migration period. Primordial sex cells varied in diameter from nine to 128 micra, and, contrasted with other cells, were spherical or ovoid with very definite cell-outlines. The nuclei seemed to conform to the general shape of the cells. Richards and Thompson observed in *Fundulus* no peculiar invagination of the nuclear membrane such as was reported by Dobbs ('10). An unusually large centrosome plainly visible in the cytoplasm was always characteristic of these cells. In older embryos germ cells were recognized by their size.

Positive identification of primordial sex cells was made in a twenty-four-day embryo in which they were seen in sac-like anlagen of the reproductive organs dorsal and slightly lateral to the hind gut, numerically inferior to the cells surrounding them. From this stage their path was followed backward through all intermediate phases of migration, until they were no longer evident. At forty-six to

fifty hours the position of the germ cells was striking, being widely distributed throughout the embryo, a fact also recorded by a number of other observers.

The authors considered that observation of these early embryos revealed several important facts: the primordial germ cells were as truly characteristic and as easily recognized as any found in the germ glands of later stages; they were located in the posterior half of the embryo, becoming gradually more numerous as the anterior part of this region was approached; laterally they ranged from the extra-embryonic tissues to within the lateral mesoderm and the edge of the developing gut. In general the progress along the "germinal path" was directly proportional to the developmental stage of the embryo.

They believe that the early distribution and migration of sex cells is best explained by the forces of growth, that is, the streaming of organ-forming tissues which contribute materials to different parts of the embryo. They consider of great significance the fact that no sex cells were found in that part of the embryo which develops from the head fold. The germinal path led from the peripheral entoderm into the border of the undifferentiated entodermal cell mass. By the time the gut was formed these cells were lateral to it, and they all eventually became located in the splanchnic mesoderm of this region. From these they migrated dorsal to the gut to a region ventral to the Wolffian ducts. Here they became surrounded by peritoneal cells which formed the somatic portion of the gonad. From this position the germ-gland anlagen were shifted back to their final position dorsal to the gut. Such is the story of the primordial germ cells according to these authors, and in conclusion they say "that evidence derived from this study of *Fundulus*

is in absolute harmony with the theory of early segregation of primordial germ cells." ('12, p. 339).

The work of Cowperthwaite

An interesting approach to the problem of the origin of definitive germ cells was made by Cowperthwaite ('25) in which the occurrence of meiotic phases was considered the criterion of a definitive oocyte.

The first series of ovaries studied was taken from a group of rats ranging in age from newly-born to eight days. This group was selected because the later phases of meiosis are known to occur in oocytes during this period. A second series was taken every ten days from the tenth day after birth to the ninetieth day, thus including ovaries from individuals at the time of weaning, puberty, and sexual maturity. A third series was secured from mated rats. The birth date of the first litter was recorded, and the litter was taken from the mother. Using Donaldson's ('15) information that ovulation occurs in the rat twenty to forty-eight hours after parturition, the females were allowed to mate again at once. The second litter was removed immediately as before. This was done in order to avoid the lactation inhibition of oestrous activity, since it was desired that females undergo normal oestrus in the presence of the male. Ovaries were preserved from females at the time of the second parturition and on the first, second, third, fourth, fifth, and sixth days thereafter. In this way it was hoped to cover the entire oestrous cycle.

Early meiotic phases occur in embryonic ovaries, and at the time of birth the thick threads of the pachytene stage appear. Cowperthwaite's studies began at this point. By the end of the fourth day post-partum, meiosis had been completed and no transitional stages were to be found

"between the undifferentiated germinal epithelial cells and the post-meiotic germ cells." A study of size differences and nuclear condition of small as compared to large oocytes led to the conclusion that the smaller follicles represent a retarded growth condition and that they are not derived from a new germ-cell formation as many have supposed. This conclusion was reached by the author chiefly because of a failure to find "fresh meiotic phenomena in the germinal epithelium either at this age or at any succeeding period in the series of ovaries studied." ('25, p. 79).

In the rat a new oestrous cycle normally occurs directly after a parturition. Ovulation, which takes place at the height of the cycle, may be expected to occur from twenty to forty-eight hours after the birth of a litter. With this in mind Cowperthwaite made observations on a series of ovaries which covered the entire cycle. Contrary to the findings of Allen ('22, '23) no evidence was found throughout the series that new germ cells are proliferated periodically from the germinal peritoneum. The only possible evidence of periodicity was found in the observation that more cells were seen enlarging *in situ* in the ovaries preserved near the time of parturition, and on the fifth day thereafter. Since each of these periods corresponds to the beginning of a new oestrous cycle, and resting cells would, therefore, be entering a growth period preparatory to ovulation at the height of the cycle, Cowperthwaite considered this periodicity adequately accounted for. In view of the significance of meiotic phases in the history of germ cells, she concluded that oogenesis is not continued during pre- and post-pubertal life, and new germ cells are not proliferated periodically from the epithelium.

Duesberg in 1908 made a study of

spermatogenesis in the white rat, but, for some reason, found no indication of synapsis or other meiotic phases.

The work of Swezy

Swezy ('29a), on the other hand, records observations on maturation in the male rat of a distinct and prolonged synapsis which occurred just before synizesis.

In the female rat ('29b) Swezy found ova arising by proliferations from the germinal epithelium, all the cells of which she believes are potential ova. According to Swezy this proliferation begins with the differentiation of the gonad and may last as long as 369 days after birth. The embryonic ovary is filled with ova which undergo typical maturation phases. Meiosis continues until five days after parturition. But the ova, Swezy believed, degenerate, since none was found in the ovary of the twenty-day rat. After the fifth day no typical maturation phases were present. Swezy says: "With the degeneration of the embryonic ova the ovary takes on adult structure. The ovary of the adult female rat shows the typical phases, indicating that this is the primitive type, with the modified form an acquired characteristic." Swezy is particularly interested in chromosome numbers in mixed rat strains.

Two recent papers by Swezy and Evans ('29a, '29b) report studies on maturation of human embryonic ova and of ovogenesis in several mammals, the guinea pig, the cat, the dog. In human embryos of the third month early maturation phases of the ova were found. These phases consisted of typical formation of leptoneura, synizesis, pachynema, and diploneura. Prochromosomes, similar to those of insects, were found in leptoneura which later resolved into leptotene threads, a phenomenon hitherto not observed in mammals. In embryos of five and one-

half months all these prochromosomes had disappeared. Swezy and Evans believe that these embryonic germ cells all disappear before adult life is reached, and that the ova developed during adult life do not pass through these phases preliminary to maturation.

From observations on the guinea pig, cat and dog, these authors conclude that oogenesis occurs throughout adult life as a rhythmical process, and that during the life-time of the individual, literally thousands of ova are produced *de novo*. Such a conclusion recalls the results obtained by Allen ('22, '23) in the mouse. In the guinea pig, cat, and dog the rhythmical proliferation of new cells from the germinal epithelium coincided with the oestrous rhythm. Though it is difficult to make this correlation in man because of a lack of knowledge of the cycle, Swezy and Evans believe that ultimately such a coincidence will be found for man as well as other mammals.

The conclusions arrived at here substantiate the work of Swezy, as is indicated by the following: (Exp. Biol. Med., 27, p. 11).

New sex cells are produced by proliferations from the germinal epithelium in the form of invaginations and ingrowths of epithelial cords. These become separated from the germinal epithelium, pass through the tunica albuginea and form a more or less continuous layer underneath the tunica. From one to many cells in each group may develop into ova, the remaining forming the follicle cells.

Contrary to the concept involved in the germ plasm theory, the mammalian ova (excepting those that mature and are fertilized) have a shorter life-span than any other group of cells in the body outside of the reproductive tract.

Willier ('26) identified primordial germ cells outside the chick embryo (extra-embryonic) and designed experiments to determine whether they were essential for gonad development, and whether the gonad would develop any germ cells in

the absence of the primordial germ cells. The blastoderm of chick embryos incubated nineteen hours was removed and the area pellucida isolated so as to be free of all primordial germ cells. The isolated area pellucida was implanted in a host embryo of nine hours incubation. After nine days, histological examination showed the anterior part of the embryo well developed: large brain vesicles partially surrounded by cartilage, medulla, ganglia, pigment layer of the eye, bone, gut, oral cavity, hypophysis, muscles, etc., but the more posterior parts of the embryo were absent entirely or very poorly developed. The entire absence of a gonad was striking.

Richards, Hulpieu, and Goldsmith also in 1926 investigated the history of germ cells in a series of chick embryos from the beginning of incubation to 180 days after hatching. The early development as described by these authors is entirely in accord with that described by Swift ('14, '15, '16). The primordial germ cells arise in the extra-embryonic region and are carried in the blood stream to the gonadal ridge. In the male from the eleventh day of incubation, division of sex cells took place actively with no signs of degeneration, although their history was followed for seventy-five days. An even more complete series was available in the female, and no transformations of peritoneal cells into germ cells were observed. The history of developing ova is purely one of growth, division, and preparation for maturation. These authors are confident that the definitive ova are all traceable to early-segregated germ cells without degeneration and without contributory proliferations from the germinal epithelium. Small cells from the peritoneum go into the formation of the follicles but not of the definitive ova.

Woods ('25, '29) made observations on

living and sectioned material covering the various stages in the life-cycle of *Spaerium striatinum*, the viviparous bivalve, and concluded that the germ-cell history was traceable from the fertilized egg to sexual maturity. He divided the cycle into six general periods with fairly definite limits. Primordial germ cells of characteristic structure appeared just before gastrulation. One large germ cell appeared in the mesoderm mass on either side of the blastocoele, and of these, according to Woods, all germ cells are direct descendants. The ectomesoblasts, he thinks, contribute nothing to the formation of germ cells. Metamorphoses of somatic cells into germ cells are not observed in the material studied. During maturation certain granules appeared in the cytoplasm of the ovum. During cleavage these granules segregated into those cells which give rise to germ cells. Woods is particularly interested in these granules, their origin, nature and significance.

From an investigation of germ-cell history in the teleost, *Cottus bairdii*, Giraid, Hann ('27) concluded that definitive germ cells in both sexes have their origin only in primordial sex cells, since no transition from somatic cells to germ cells was observed at any stage. Hann thinks the original source of primary germ cells is the entodermal giant cells first found before the gut was formed and later along the ventral and lateral margins of the gut. Some of these cells passed through the lateral mesoderm to a position dorsal to the gut, from which they were shifted to the gonadal region. This interpretation is entirely in accord with that of Richards and Thompson ('21) in their observations on *Fundulus* embryos.

Sex could be distinguished first at fifty-two days, in the female by early maturation stages and in the male by the presence of the sperm duct. A part of the oocytes

formed during the first season matures for the first spawning, which takes place at the age of two years. The remainder form a reserve supply, which is increased each year by dormant oogonia become active. In the male spermatogonia lying dormant in the cysts during maturation give rise to sperm at the next season.

The work of Humphrey

Humphrey in 1925 began a study of primordial germ cells in Urodeles. In the first report, based entirely upon morphological studies, the author states his conclusion that the primordial germ cells of the Urodeles are mesodermal in position from the time the mesoderm and the entoderm become separate germ layers. With this interpretation previous workers on Urodele germ cells, particularly Dustin ('07) and Allen ('11), are in agreement.

The early position of the primordial germ cells is described by Humphrey in *Hemidactylium* and other Amphibia. He found that these cells lie in the mesoderm just lateral to the somite. At this stage they showed no nuclear distinguishing features, but in size and in abundance of yolk, they were equal to the germ cells of older embryos. Later these cells were seen crowded medially against the entoderm. At this time nuclear peculiarities marking them as germ cells were distinguishable. During the further growth-shiftings of the mesoderm, these cells were carried medially and came to lie in the genital ridges on each side of the gut.

Humphrey ('27, '28, '29) next carried his studies into experimental work on the germ cells of *Amblystoma*, approaching the problem from a somewhat different angle. Mesodermal cells and large cells thought to be primordial germ cells were transplanted to the lateral body wall of the embryo. In five out of seven cases these transplanted primordial germ cells gave

rise to a gonad on the site. The author concluded that "primordial germ cells may survive, differentiate, and produce an ectopic gonad when transplanted before they become morphologically recognizable." ('27b, p. 40).

Part of the experimental work ('27a) consisted in the extirpation of the primordial germ cells of *Amblystoma* and its effect upon the developing gonad. Here Humphrey found that complete extirpation of the area of mesoderm in which the primordial germ cells are to be recognized results in the absence of the gonad.

A similar conclusion ('29) resulted from a study of sex differentiation following orthotopic implantation. The author considers that the area of mesoderm of *Amblystoma* in which germ cells are recognized may be regarded as the preprimordium of the gonad, since implantation of this area results in the development of a gonad. The area extends from the level of the eighth or ninth somite to that of the sixteenth or seventeenth, and is intermediate between the axial and lateral divisions of the mesoderm. Humphrey believes that the primordial germ cells are mesodermal in derivation and must be located in the mesoderm from the time the germ layers are first separated.

The work of Goldsmith

Goldsmith ('28) in tracing the history of the procreation cells in the domestic fowl found large size, spherical shape, the presence of an attraction sphere, and clear staining reaction of the nucleus reliable criteria for identifying germ cells. Primordial germ cells were first seen in the embryo during the primitive streak stage at the outer edge of the proamnion anterior and antero-lateral to the head fold. Before the mesoderm formed they were found in the space between the entoderm and the ectoderm. But later as the mesoderm

grew into space the primordial germ cells became incorporated in it and by their own movement found their way into the blood vessels. Up to the thirty-three hour stage of incubation they were found only in extra-embryonic tissues. Goldsmith figures primordial germ cells within the blood vessels of the splanchnopleure of a twenty-four hour embryo, and at various locations in later stages. He points out in this connection the correspondence between his observations and

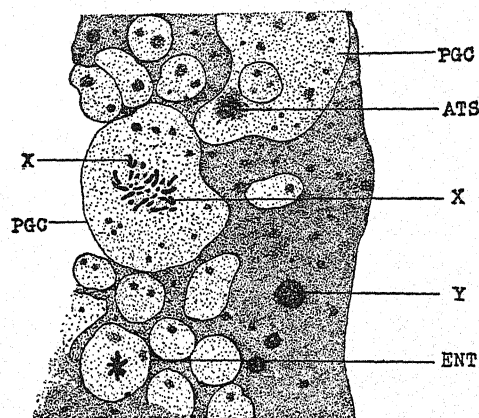


FIG. 10. SECTION THROUGH THE REGION ANTERIOR TO THE HEAD FOLD, SHOWING THE POSSIBLE PRIMORDIAL GERM CELLS STILL EMBEDDED IN THE ENTODERM. SHOWS GREAT DIFFERENCE IN SIZE BETWEEN THE PRIMORDIAL GERM CELLS AND SOMATIC CELLS

ENT—entoderm cells. X—sex chromosome. PGC—primordial germ cell. Y—yolk. ATS—attraction sphere. After Goldsmith in *Jour. Morph. and Physiol.*

the findings described by both Dantschkoff ('08) and Swift ('14).

When the embryonic and extra-embryonic blood systems joined, the primordial germ cells were found in the embryo itself (at thirty-three-hours incubation). Wide distribution of the germ cells throughout the embryo was evident until about the forty-hour stage, when they become more numerous at the site of the gonad, though at this stage many were still present in the blood stream. They gradually took

up residence in the developing germinal epithelium, and by the sixth or seventh days sex could be determined reasonably and accurately, though for absolute certainty the chromosomal complex alone is reliable. In the male cells two large V-shaped chromosomes were present while the female cells showed only one.

Goldsmith observed no "wide-spread degeneration of the primordial germ cells of either sex" and places confidence in the belief that these primordial germ cells appearing in the early embryonic stages

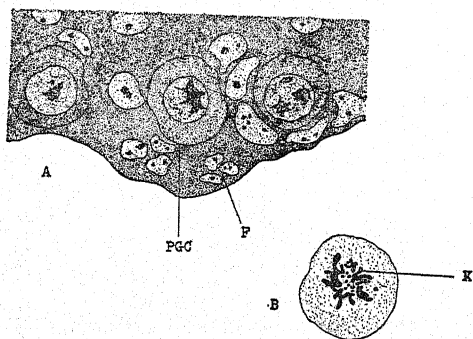


FIG. 11. A—A SECTION THROUGH THE OVARY OF A SEVEN-DAY EMBRYO SHOWING THE PRIMORDIAL GERM CELLS PLACED IN THE GERMINAL EPITHELIUM. THE THICKNESS OF THE EPITHELIUM IS INDICATIVE OF A FEMALE. B—A SINGLE GERM CELL SHOWING METAPHASE PLATE

F—follicle cell. PGC—primordial germ cell. X—sex chromosome. After Goldsmith in *Jour. Morph. and Physiol.*

maintain their identity, and "continue through to form the definitive germ plasm."

Stromsten ('29) has studied the history of germ cells in the goldfish. His observations favor the theory that the germ cells migrate through the dorsal mesentery to their destination beneath the floor of the swim bladder.

THE BEARING OF REGENERATION ON THE ORIGIN OF THE GERM CELLS

Aside from the purely cytological aspect, an interesting approach to the

problem of the definitive germ cells has been made from an entirely different standpoint, that of regeneration of the gonad following removal. Swingle bordered on this idea in his 1921 paper on the germ cells of Anurans, when he said:

... Certainly this is the more probable view [that primordial germ cells of the tadpole alone give rise to the definitive sex cells of the adult frog], though the burden of proof rests with those of us who hold that the *Keimbahn* is continuous. . . . It would seem from this that the crux of the whole problem is to determine whether or not germ cells can develop in an organism after the primordial germ cells have been destroyed. If they do develop, then the doubtful question of the transformation of mesothelial cells into germ cells is settled in favor of the mesodermists, but if they do not develop, and the gonad is sterile and remains so up to the period of sexual maturity, then the decision is in favor of the entodermists ('21, p. 290).

The work of Willier ('26) previously mentioned, is interesting in this connection. It brings evidence that in the chick no germ cells develop in the absence of primordial germ cells. Where the areae pellucidae were isolated free of all germ cells, the entire absence of the gonad was striking.

Regeneration in Coelenterates has been considered dependent upon the presence of latent germ cells such as Weismann ('93) found in the ectoderm of Hydromedusae. Weismann took the position that regeneration is due to the presence of germ plasm, since that is the only substance which can give rise to all parts of the body. Montgomery ('06) and Hegner ('14) accept the germ-cell explanation, believing that regeneration in Coelenterates is due to widely distributed germ cells. Hargitt ('16, '17, '18, '19), however, found no direct evidence in favor of this view. He concluded that "the great body of facts concerning regeneration in many phyla contradict such an interpretation. Especially do the observations upon regeneration from iso-

lated cells of hydroids disprove the germ-plasm theory." Hargitt, confirming Willson ('13) explains regeneration thus: "they [isolated cells] become despecialized into potentially embryonic cells and probably from this change have acquired their regenerative capacities."

Morgan ('01), after discussing a considerable number of theories of regeneration, also rejects the germ-plasm theory completely, finding many facts of regeneration which are incompatible with such an explanation.

Castle and Phillips ('11, '13) removed ovaries from a series of seventy-four guinea pigs and seventeen rabbits. The tube so far as possible was left intact. "Ten animals showed regenerated ovaries and three had young. Forty-two showed at post-mortem complete atrophy of the genital tract and absence of ovarian tissue." ('11, p. 8). In a later paper ('13) these authors offer a summary of their experiments on 141 female guinea pigs:

"In eleven cases ovarian tissue was regenerated at the original ovarian site and in three of these cases young were produced having the genetic characteristics of the mother."

The work of Davenport

In connection with studies dealing with fecundity and ovarian transplantation, Davenport ('25) performed a series of ovariectomies in mice. As the experiments progressed it became evident that ovarian tissue was again present at the site of the operation. This discovery led to a study of regeneration, and Davenport was interested in answering the following questions:

"Under what conditions does regeneration occur and what conditions inhibit it? What is the site of the regeneration? Are young produced from eggs derived from the regenerated ovary?" ('25, p. 1).

In the first series, consisting of thirty-one operated mice from which thirty-eight ovaries were removed, both the capsule containing the ovary and the coiled Fallopian tube were excised. In the second series, comprising ninety operations, the capsule was "slit open opposite to the stalk and folded back, exposing the ovary. The ovary was then removed with as much of its short stalk as feasible." ('25, p. 2).

Sixty-four per cent of the operations were followed by more or less complete reappearance of the ovary. From Davenport's analysis it appears that the proportion of regeneration increased directly with the interval elapsing between the operation and the examination, from about nine weeks to twenty-five weeks. After seven months, however, the proportion decreased, and Davenport suggests as a possible explanation that the regenerated ovaries might have been absorbed in the later months. The age of the animals seemed to have no clear effect, though Davenport observed that regeneration rates for mice between nine and ten weeks of age were relatively low, while some at four weeks gave as high as eighty-three per cent. Ages ranged from one to four months.

The ovary usually regenerated at the site of the one removed, though in some cases the regenerated ovary was located caudad to the tube, seeming to indicate that regeneration may take place as much as five or six millimeters distant from the operated site. Usually no embryos were found in the horn of the uterus on the operated side, but corpora lutea were frequently found in regenerated ovaries, and in some few cases embryos were found in the horn of the operated side.

In fourteen cases no trace of the capsule could be found at autopsy, and yet ovarian tissue was present. Davenport considered this strong evidence that regenera-

tion of the ovary may take place from tissue proximal to or lateral to the stalk. He also considered that this observation indicated that the old ovary had been completely removed and the new formation was not merely an enlargement of a fragment of the old ovary that had been left in place. No histological verification of this claim was attempted; macroscopic examination of masses of tissue at or near the site of the operation was the criterion of regeneration. According to the writer's observations, which will be described subsequently, the absence of a capsule at autopsy in adult rats is no indication that complete ovariectomy was accomplished.

The presentation by Hargitt of his observations on germ-cell history in the male rat at the Kansas City session of the American Association for the Advancement of Science in 1925 was followed by a discussion of the evidence for germ-cell continuity in general. At this time Davenport suggested that even if germ cells do arise from soma cells, we are still dealing with a continuity of chromosomes, since the chromosomal complex of somatic cells is descended directly from germ cells; and that this "saves the day" for continuity. He pointed out that it is the cytoplasm of the cells which takes part in differentiation into specialized body cells. In the course of the general discussion the idea was advanced that the interaction between the nucleus and the cytoplasm of a cell is sufficient to render such a conclusion questionable.

The work of Parkes and his associates

Indirect evidence for proliferations from the germinal epithelium comes from studies by Parkes ('26, '27, a, b, c,) and Brambell, Parkes and Fielding ('27 a, b, '28) of the effects of irradiation in the mouse, though no very definite claim is made by these authors that the cells

which were proliferated after partial or complete sterilization were germ cells.

Parkes found that when the young female is irradiated at three weeks of age (Part I) the result is complete degeneration of ova, granulosa cells, theca interna, where it has differentiated, and that the ovary subsequently comes to consist almost entirely of extra-follicular tissue, that is, of proliferations from the epithelium. In animals irradiated at birth (Part II) the course of events is similar to that found in those irradiated at three weeks old, but "in some few instances the proliferation from the epithelium becomes extremely luteal-like." An interesting age difference was apparent when adults were irradiated, namely, that while irradiation of the adult obliterated all follicles, as in young animals, no post-irradiation proliferation of tissue from the germinal epithelium took place. Parkes was interested here not in demonstrating that these proliferations did not consist of germ cells, but in the occurrence of the oestrous cycle after X-ray sterilization and subsequent follicular degeneration, showing that neither the follicle nor the corpus luteum is necessary for the maintenance of the oestrous cycle. However, from Parkes' description of the post-radiation proliferations, one concludes that they consisted entirely of extra-follicular tissue.

The work of Brambell, Parkes, and Fielding was similar in procedure to that of Parkes. Simultaneously with the degeneration of the follicles, the inter-follicular tissue atrophied and the germinal epithelium proliferated epithelial cords. In the adult animals the ovaries were composed almost entirely of this first proliferation. In many cases a second proliferation from the germinal epithelium followed. These resembled the so-called spermatic cords described by some authors in the ovaries of rabbits and free-martin

cattle, or structures called by many "anovular follicles." That these authors consider the possibility that some cells of these proliferations may be ovular follicles is indicated by the statement that the "post-irradiation proliferations might correspond to the definitive proliferations of the normal ovary described by de Winiwarter and Sainmont" ('09). ('27 a, p. 111.)

The same age differences as reported by Parkes were observed by these authors ('28). Irradiation of the adult during pregnancy produced a rapid degeneration of oocytes and larger follicles, but none of these animals showed any signs of proliferation and ingrowth from the germinal epithelium such as was described in animals irradiated before puberty. Also when adult animals were irradiated during lactation the germinal epithelium remained thin and inactive.

One series of experiments was initiated with a view to ascertaining whether after sterilization and unilateral ovariectomy at three weeks old, the remaining (sterilized) ovary hypertrophies as is true in normal unilateral ovariectomy. While the results are insufficient for very definite conclusions, there seemed to be a true compensatory hypertrophy of the ovary. No indication is given as to the source of the cells or whether the authors considered the proliferated tissue germinal.

In 1926 Parkes and Bellerby conducted a series of ovariectomies on mice in connection with work on injection of the oestrus-producing hormone. These authors state that their findings on regeneration confirm those of Davenport, the criterion of regeneration being the spontaneous reappearance of oestrous phenomena. They considered the possibility of regeneration so great as to prejudice the hormone-injection tests which were the original purpose of their experiments.

Later ('27) a paper appeared by Parkes,

Fielding, and Brambell on regeneration after double ovariectomy, continuing the method of Parkes and Bellerby. The oestrous cycle in eleven animals ceased after double ovariectomy for a longer period than could be accounted for by an unusually long dioestrous interval, and since only a very small amount of ovarian tissue is required to maintain oestrus, this complete cessation was considered by the authors to indicate removal of ovarian tissue. The extirpated ovaries were fixed and sectioned to give histological evidence of complete removal.

Vaginal changes characteristic of the oestrous cycle recommenced in all eleven animals. In eight of these cases ovarian tissue was demonstrated histologically. One was not available for observation, and the remaining two failed to show any regenerated tissue. However, the authors consider that since oestrous phenomena recommenced some small bit of ovarian tissue must have been present which was overlooked in dissection. In four animals the oestrous cycle did not return and no regenerated tissue could be detected from a study of serial sections of the ovarian region. The total number of animals involved was 121, each doubly ovariectomized. The above described operations consisted of removal of ovaries, capsules, and portions of the tubes.

Tamura ('27), in a study of implantation of ovarian grafts in the male mouse, found that the success of the grafted tissue depended primarily upon its vascularization and secondarily upon the activity of the germinal epithelium of the graft itself; and that about sixteen days after transplantation a new proliferation of cells from the germinal epithelium occurred which gave rise to young oocytes. Grafts were made into the kidney of the male rat, the surface of the kidney being slightly injured to receive the graft.

Tamura's results demonstrated to his

satisfaction that transplantation of ovarian tissue into male mice was successful in ninety per cent of the cases (thirty-one mice, total number of experimental animals), and "in almost all these cases the germinal epithelium remained intact." ('27, p. 157). Tamura observes that these conclusions are supported by those of Schultz ('00) and of Voss ('25) in the guinea pig, contrary to the results of Marshall and Jolly ('07), who stated that in their experiments the germinal peritoneum was always absorbed. In a great number of Tamura's grafts mitotic figures were present in the germinal epithelium at about eight days after transplantation. These are similar to those observed by Allen ('23) in cyclic proliferations from the germinal epithelium at each normal oestrous period. In addition "young oocytes and successive stages of neoformation of the oocytes" were found, and Tamura believes this proliferation of cells quite comparable to those observed by Allen.

Even in the less favorable grafts where degenerative changes set in among the primary follicles, if vascularization had been established, the germinal epithelium was still active, an observation to which Tamura attached considerable importance. Young oocytes appearing before the tenth day became medium-sized follicles at about fourteen to fifteen days, and proliferation continued up to twenty days. At this point the graft attained the stage at which it was when transplantation took place, and the activity of the epithelium ceased until the second proliferation. The rhythm, however, was slower than that of the normal oestrus cycle of the female as recorded by Allen. Tamura has little doubt apparently that the source of these proliferations was the epithelium.

In working on the problem of sex-inversion in the domestic fowl, Domm ('27)

was led to perform an extensive series of gonadectomies on hens. Subsequent examination revealed in a number of cases a regeneration of ovarian tissue. These Domm attributed to incomplete removal in consequence of the difficulties inherent in such an operation in the fowl. Some operations were known to be incomplete at the time of removal and regeneration was to be expected.

Domm reports some cases, however, in which regeneration followed apparently complete ovariectomy despite the fact that the ovarian region had been thoroughly cauterized. The tissue regenerated was functional to such an extent as to interfere seriously with the object of the operation. With regard to these particular cases Domm concludes that a very small fragment of ovarian tissue must have been left in place. He says: "the mass of ovarian tissue which remained behind must have been extremely small, in fact, in some cases one would wager that they were so small as to be almost invisible. Nevertheless, such fragments hypertrophy and counteract the effects of complete ovariectomy." ('27, p. 98).

An experimental study of ovarian regeneration in mice was made by Haterius ('27, '28) basing conclusions on histological study. The operative procedure was refined and precaution taken that the capsule be slit and that as little non-ovarian tissue as possible be removed. In some few cases the capsule and a part of the stalk were included in the excised tissue. To test the regenerative capacity of ovarian tissue in mice partial operations were performed. Incomplete removal was always followed by striking hypertrophy of the remaining piece, a fact also recorded by Kanel ('01), Hartman ('25), Lipschutz ('25), Slonaker ('27), and others.

Adams and Kirkwood ('28) performed gonadectomies on both males and females

of the salamander, *Triturus viridescens*, and noted, after varying periods of time, the presence or absence of gonadal tissue, the condition of the reproductive ducts, and changes in the secondary sexual characters. Of seventy-two males, examined from thirty-three days to a year after castration, sixty-four showed no testicular tissue, five showed one lobe on either right or left side, and three a lobe on each side. At the time of this first report, the evidence was being examined whether these eight cases were due to regeneration or to incomplete removal. In the sixty-four cases where no testicular tissue appeared, the Wolffian ducts and ureters were atrophied to various extents. Of nineteen ovariectomized females, examined fifty-eight to 192 days later, ovarian tissue was present in only one. All the females showed atrophied oviducts.

During the preparation of this review, an abstract describing recent experiments by Pencharz ('29a, '29b) has come to the writer's attention. Bilateral ovariectomy was performed on a total of 118 animals including both rats and mice. The age range was from twenty-five to 180 days and the period of observation seventy-five to 308 days. Complete absence of oestrous phenomena followed in all except three individuals. In these three, oestrous cycles continued, and study of serial sections of the ovarian region demonstrated incomplete removal. Contrary to the opinion of Parkes, Fielding, and Brambell ('27), Pencharz concludes that "an initial absence of cycles is not evidence of the completeness of the removal of the ovary." ('29, Wistar Institute Abstract, no. 2322, July 31). His observations led him to believe that ovarian tissue does not arise from non-germinal substance but that even a very minute fragment left intact may become extensively hypertrophied and in the natural course of events functional.

THE AUTHOR'S EXPERIMENTS ON OVARIAN
REGENERATION IN THE ALBINO
RAT

The immediate occasion for this review was an extensive study of regeneration in the albino rat. This work was begun in November, 1926, with a view to determining under what conditions the operator can be certain of complete removal, whether after such removal regeneration is possible, and what bearing the age of the animal has upon regeneration.

As a preliminary series, both ovaries were removed from 105 rats and each ovary was preserved for later histological study. The animals, which in this first series ranged in age from ten to two hundred days, were selected from a well-cared-for colony originally derived from Wistar Institute stock. Operative technique was simple but carefully carried out, ordinary aseptic precautions being taken to prevent possible infection. Usually both sides were operated at the same time, but occasionally, when it seemed advisable, from one to three days elapsed between the two ovariectomies. To avoid the possibility of death from anaesthesia standardized hospital ether was used, and the amount of anaesthetic administered reduced to a minimum. Small incisions were made through the skin and body wall above the ovarian region on each side of the back. Operations were performed under a powerful magnifying glass. The thin, transparent capsule of the ovary was "picked up" by means of forceps and slit with fine iridectomy scissors. The ovary was cut off at the hilus, the stalk and capsule being left in place. The tubes were injured as little as possible, and in no case were they ligated. The wounds were sutured with surgical silk and swabbed with iodine and collodion. With the exception of one or two cases recovery was rapid and uneventful.

The period allowed for regeneration ranged from ninety to 180 days. Among the 105 doubly-ovariotomized rats (210 possibilities), there were eight cases of regeneration as determined by sectioning the regenerated masses of tissue. None of the rats under forty days showed regeneration, although rats from ten to forty days of age at the time of operation were allowed the longer period in which to regenerate. The eight ovaries removed from these sites of regeneration were sectioned to determine whether the entire ovary had been removed. In two of these eight original ovaries incomplete removal was demonstrated histologically, while in six cases, extirpation was apparently complete (see Fig. 12). This gives a regeneration rate of 2.88 per cent in the rat as compared to sixty-four per cent obtained by Davenport ('25) in the mouse, five per cent by Haterius ('27), 16.6 per cent by Pallot ('28), and 3.46 per cent by Parkes, Fielding, and Brambell ('27) also in the mouse, where the ovary, capsule, and a portion of the tube were removed, fifteen per cent where only the ovary was removed.

The histology of the ovary

The adult ovary consists histologically of a frame-work of stroma and strands of connective tissue radiating out from the hilus. In this frame-work the Graafian follicles are embedded, and the whole is invested by a serous covering. Though this serous membrane or capsule is derived from the peritoneum, it differs essentially from that structure in so far as its epithelium consists of a single layer of columnar cells instead of the flattened endothelial cells of the peritoneum of other parts. This covering was termed the germinal epithelium by Waldeyer.

The frame-work or stroma of the ovary is composed of a characteristic soft tissue

abundantly supplied with blood vessels. It consists for the most part of small, spindle-shaped cells, with connective tissue strands between. On the surface of the ovary this stroma is much condensed, and forms a more compact layer. This was formerly regarded as a distinct fibrous covering and was called the "tunica albuginea," a term which still is used widely. It is really nothing more than a condensed layer of the stroma.

Numerous Graafian follicles are embedded in the stroma. Immediately beneath the "tunica albuginea" the follicles in the earliest condition are found and this is termed the cortical layer or cortex. But in an ovary from the surface of which ovulation is taking place regularly, and one in which, therefore, corpora lutea appear, more mature follicles are seen side by side with younger follicles. Some atretic follicles are always present. Toward the center of the ovary the stroma becomes highly vascular, and this region is called the medullary region. It was called by Waldeyer the "zona vasculosa." This stroma forms the tissue of the hilus by which the ovary is attached (the stalk).

The histology of the regenerated bodies

The regenerated bodies in the six occurrences described here consisted of irregular masses of interstitial tissue (stroma) alternated with fibrous tissue. In some cases regenerated masses were not surrounded by a capsule as is the original ovary; and in some others the slit capsule had healed over, enclosing the regenerated tissue. Contrary to the findings of Davenport, these observations showed no apparent correlation between the presence of the capsule at autopsy and the complete removal of the original ovary. Where no regeneration took place at the site of the excised ovary the capsule was found frequently at autopsy adhering to the tube.

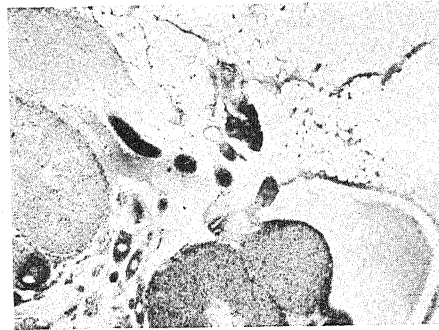
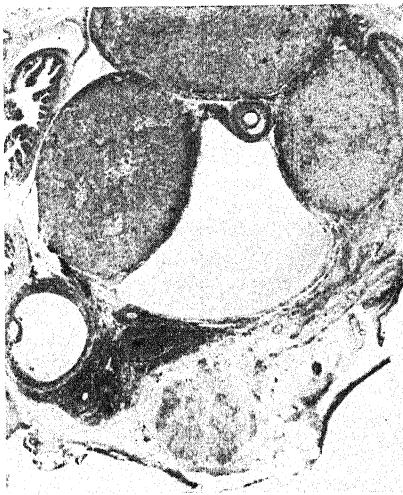


FIG. 12. PHOTOMICROGRAPHS SHOWING MICROSCOPIC APPEARANCE OF A TYPICAL REGENERATED BODY OF THE FIRST SERIES

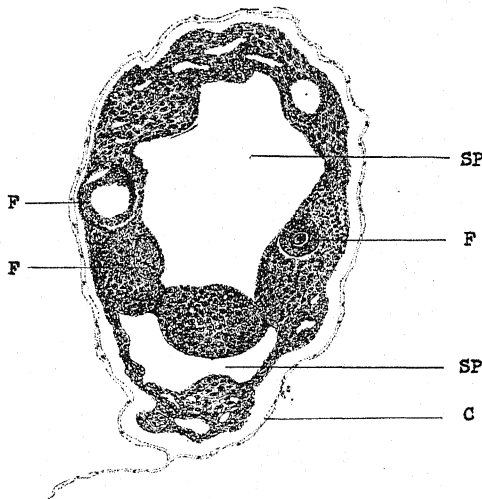


FIG. 13. SECTION THROUGH REGENERATED BODY SHOWING SPACES FILLED WITH CLEAR FLUID WHICH TAKES A SLIGHT STAIN. GERM CELLS IN THE TISSUE SURROUNDING THE SPACE

SP—space containing fluid. C—capsule of ovary.
F—follicle.

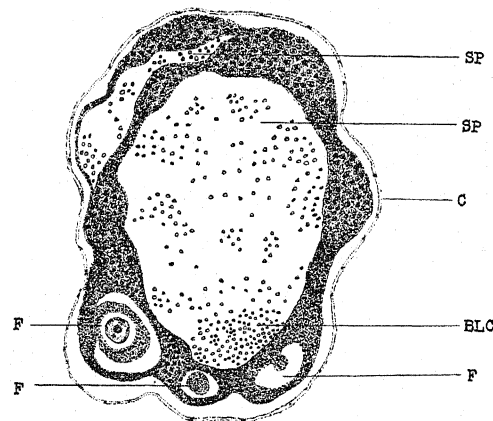


FIG. 14. SECTION THROUGH REGENERATED MASS SHOWING SPACES FILLED WITH BLOOD CELLS

F—follicle. SP—space filled with blood. C—capsule of ovary. BLC—blood cells.

Some sections show cut ends of the Fallopian tube, as if the body had regenerated at the terminus of the tube, and had adhered to it so that in dissecting out the regenerated body a portion of the attached

tube was also excised. Frequently great hollows are seen in regenerated masses of tissue either filled with a fluid which takes a light stain and in which no cells appear, or filled with many blood cells. Cross-sections of blood vessels are numerous in the sections, and fatty tissue is always present in the regenerated masses,



FIG. 15. PHOTOMICROGRAPH SHOWING APPEARANCE OF TYPICAL NON-GERMINAL REGENERATED MASS

occasionally in great abundance. In some of the bodies germ cells are small and scattered, while in a few the follicles are more advanced and fairly widely distributed. In the two cases in which incomplete extirpation can be demonstrated, the regenerated bodies are much larger and have an appearance nearer to that of



FIG. 16. PHOTOMICROGRAPH SHOWING INTERSTITIAL AND CONNECTIVE TISSUE COMPOSING NON-GERMINAL REGENERATED MASSES

normal ovarian tissue, indicating that where a piece large enough to be detected by sectioning the excised ovary is left at operation, the hypertrophy is striking.

Frequently a thin capsule filled with a fluid was found at the site of regeneration. These invariably collapsed when punctured, and contained either blood (haemocoel) or a clear, watery fluid (hydrocoel) similar to that found in spaces within the regenerated bodies. With the exception of one case, no germ cells were present in the tissues surrounding such a collapsed capsule. In one a small body, consisting



FIG. 17. PHOTOMICROGRAPH SHOWING APPEARANCE OF NON-GERMINAL REGENERATED MASS

of scattered, early follicles and stroma, was present at the edge of the capsule.

Where no regenerated tissue was found at autopsy, the uterus appeared small and white, showing no vascularity whatsoever, the usual condition in castrated animals. Vascularity of the uterus was, however, associated with the occurrence of a hydrocoel or a haemocoel regardless of the presence or absence of a tissue-mass containing germ cells. In one instance vascularity of the uterus was prominent when the regenerated mass showed interstitial tissue but no germ cells, and when no hydrocoel or haemocoel was present, an

TABLE 1—*Continued*

FEMALE NO.	AGE AT OPERATION IN DAYS	DATE OF OPERATION	DATE OF AUTOPSY	AUTOPSY FINDINGS		REMARKS
				site right ovary	site left ovary	
White 180	62	1- 1-27	5-21-27	N	N	
288	62	1- 1-27	5-21-27	Large hydrocoele	N	Hydrocoele contained watery fluid, no follicles.
2348	62	1- 1-27	5-21-27	N	N	
Hooded 3	58	1-28-27	4-24-27	N	N	Female died 4-24, digestive disturbance.
4	58	1-28-27	5-21-27	N	Small body	Uterus vascular. Body consists of fatty tissue, no germ cells.
5	58	1-28-27	5- 9-27	N	N	Female died, 5-9, pneumonia.
6	58	1-28-27	5-20-27	Hydrocoele, small, white body	N	Uterus vascular. Body fatty tissue and fibrous tissue. No follicles.
7	48	1-28-27	5-24-27	Body	N	Uterus very vascular. Body has germ cells and corpora lutea. Two very small embryos in right horn.
8	48	1-28-27	5-24-27	N	N	
9	48	1-28-27	5-24-27	N	N	
10	48	1-28-27	5-24-27	Small body and hydrocoele	N	Uterus slightly vascular; hydrocoele filled with fluid; no follicles.
White 478	62	1-29-27	5-24-27	N	N	
477	62	1-29-27	5-24-27	N	N	
390	74	1-29-27	5-24-27	N	N	
347	91	1-29-27	5-24-27	N	N	
459	70	1-31-27	5-24-27	N	N	
456	70	1-31-27	5-24-27	N	N	
460	70	1-31-27	5-24-27	N	N	
1227	47	2- 9-27	5-24-27	N	N	
346	96	2- 9-27	5-24-27	N	N	
Hooded 12	45	2- 9-27	5-24-27	N	N	
13	45	2- 9-27	5-24-27	N	N	
14	45	2- 9-27	5-24-27	N	Hydrocoele	Uterus vascular; no body.
White 489	69	2-13-27	5-24-27	Small body	N	Uterus slightly vascular; body has no germ cells.
679	45	2-13-27	5-24-27	N	N	
990	40	2-13-27	5-24-27	N	N	
890	40	2-13-27	5-24-27	N	N	
1223	41	2-13-27	5-24-27	N	N	
1224	41	2-14-27	5-24-27	N	N	
1226	41	2-14-27	5-24-27	N	N	
590	56	2-14-27	5-24-27	N	N	
1240	36	2-15-27	5-24-27	N	N	
1238	36	2-15-27	5-24-27	N	N	
1239	37	2-16-27	5-24-27	N	N	
680	44	2-16-27	5-24-27	N	N	
1233	37	2-16-27	5-24-27	N	N	
12369	35	2-17-27	5-24-27	N	N	
1246	37	2-16-27	5-24-27	N	N	
780	44	2-16-27	5-24-27	N	N	

TABLE 1—*Concluded*

FEMALE NO.	AGE AT OPERATION IN DAYS	DATE OF OPERATION	DATE OF AUTOPSY	AUTOPSY FINDINGS		REMARKS
				site right ovary	site left ovary	
White 799	74	2-18-27	5-24-27	N	N	
889	74	2-18-27	5-24-27	N	N	
689	48	2-18-27	5-24-27	N	N	
560	54	2-20-27	5-24-27	N	N	
567	55	2-21-27	5-24-27	N	N	
568	55	2-21-27	5-24-27	N	N	
579	55	2-21-27	5-24-27	N	Small body	Uterus vascular. Body has no follicles.
1379	22	2-24-27	7-31-27	N	N	
1389	22	2-24-27	7-31-27	N	N	
1278	43	2-24-27	7-31-27	N	N	
1288	43	2-24-27	7-31-27	N	N	
1289	43	2-24-27	7-31-27	N	N	
1290	44	2-25-27	7-31-27	N	N	
1367	30	2-27-27	7-31-27	N	N	
1378	30	2-27-27	7-31-27	N	N	
1450	15	2-27-27	7-31-27	N	N	
1369	30	2-27-27	7-31-27	N	N	
1370	30	2-28-27	7-31-27	N	N	
1377	30	2-28-27	7-31-27	N	N	
1346	34	2-28-27	7-31-27	N	N	
1456	17	3-1-27	7-31-27	N	N	
1457	17	3-1-27	7-31-27	N	N	
1458	17	3-1-27	7-31-27	N	N	
1459	17	3-1-27	7-31-27	N	N	
1460	17	3-1-27	7-31-27	N	N	
1467	17	3-1-27	7-31-27	N	N	
1468	17	3-1-27	7-31-27	N	N	
Hooded 15	16	3-2-27	7-31-27	Small hydro-coele	N	Uterus slightly vascular; no body.
16	16	3-2-27	7-31-27	N	N	
17	16	3-2-27	7-31-27	N	N	
18	16	3-2-27	7-31-27	N	N	
19	22	3-10-27	7-31-27	N	N	
White 1478	26	3-12-27	7-31-27	N	N	
1488	26	3-12-27	7-31-27	N	N	
1490	22	3-12-27	7-31-27	N	N	
1499	22	3-12-27	7-31-27	N	N	
1489	22	3-12-27	7-31-27	N	N	
1567	17	3-12-27	7-31-27	N	N	
1568	17	3-12-27	7-31-27	N	N	
1569	17	3-12-27	7-31-27	N	N	
1570	10	3-15-27	8-1-27	N	N	
Hooded 24	24	3-31-27	8-1-27	N	N	
25	24	3-31-27	7-31-27	N	N	
26	24	3-31-27	8-1-27	N	N	
20	22	3-10-27	8-1-27	N	N	
21	22	3-10-27	8-1-27	N	N	
23	22	3-10-27	8-1-27	N	N	
27	24	3-10-27	8-1-27	N	N	

TABLE 2

Showing the individual operative histories of the second series. N = negative

FEMALE NO.	AGE AT OPERATION IN DAYS	DATE OF OPERATION	DATE OF AUTOPSY	AUTOPSY FINDINGS		REMARKS
				Site right ovary	Site left ovary	
Hooded 58	45	1-24-28	6- 4-28	N	N	One horn of uterus sealed by adhesion; filled with a fluid.
59	45	1-24-28	6- 4-28	N	N	
122	48	1-25-28	6- 4-28	N	N	
123	48	1-25-28	6- 4-28	N	N	
89	48	1-25-28	6- 4-28	N	N	
77	50	1-25-28	6- 4-28	N	N	
68	50	1-30-28	6-15-28	N	N	
69	50	1-31-28	6-15-28	N	N	
78	50	1-31-28	6-15-28	N	N	
124	49	2- 1-28	6-15-28	Body	N	Body contains no germ cells.
128	49	2- 1-28	6-15-28	N	N	
129	50	2- 2-28	6-15-28	N	N	
130	50	2- 2-28	6-15-28	N	N	
136	50	2- 4-28	6-15-28	N	N	
138	50	2- 3-28	6-15-28	N	N	
146	50	2- 3-28	6-15-28	N	N	
147	49	2- 5-28	6-15-28	N	N	
148	49	2- 5-28	6-15-28	N	N	
168	36	2- 5-28	6-15-28	N	N	
157	38	2- 5-28	6-15-28	N	N	
158	38	2- 7-28	6-15-28	N	N	
159	38	2- 7-28	6-15-28	N	N	
White 44	50	2- 9-28	6-15-28	N	N	
46	50	2-11-28	6-15-28	N	N	
47	50	2-11-28	6-15-28	N	N	
5688	24	2-14-28	6-15-28	N	N	
5680	24	2-14-28	6-15-28	N	N	
5689	25	2-15-28	6-15-28	N	N	
Hooded 177	32.	3-11-28	6-15-28	N	N	
178	32	3-11-28	6-15-28	N	N	
180	32	3-11-28	6-15-28	N	N	
56	22	3-13-28	6-15-28	N	N	
60	40	3-20-28	6-15-28	N	N	
67	40	3-20-28	6-15-28	N	N	
69	40	3-20-28	6-15-28	N	N	
70	40	3-20-28	10- 1-28	N	N	
77	40	3-20-28	10- 1-28	N	N	
78	40	3-23-28	10- 1-28	N	N	
79	40	3-23-28	10- 1-28	N	N	
80	40	3-23-28	10- 1-28	N	N	
88	40	3-27-28	10- 1-28	N	N	
Hooded 190	40	3-31-28	10- 1-28	N	N	
199	40	3-31-28	10- 1-28	N	N	
223	40	4- 2-28	10- 1-28	N	N	
224	40	4- 2-28	10- 1-28	N	N	

TABLE 2—Continued

FEMALE NO.	AGE AT OPERATION IN DAYS	DATE OF OPERATION	DATE OF AUTOPSY	AUTOPSY FINDINGS		REMARKS
				Site right ovary	Site left ovary	
White 89	22	4-3-28	10-1-28	N	N	
Hooded 225	10	4-7-28	10-1-28	N	N	
226	10	4-7-28	10-1-28	N	N	
234	10	4-7-28	10-3-28	N	N	
235	10	4-18-28	10-3-28	N	N	
236	18	4-18-28	10-3-28	N	N	
229	20	4-23-28	10-12-28	N	N	
230	20	4-23-28	10-12-28	N	N	
White 225	20	4-23-28	10-3-28	N	N	
227	22	4-25-28	10-3-28	N	N	
228	22	4-25-28	10-3-28	N	N	
229	22	4-25-28	10-12-28	N	N	
230	23	4-28-28	10-12-28	N	N	
237	21	4-21-28	10-12-28	N	N	
238	21	4-29-28	10-12-28	N	N	
239	10	5-1-28	10-12-28	N	N	
240	12	5-3-28	10-12-28	N	N	
244	12	5-3-28	10-12-28	N	N	
245	12	5-3-28	10-12-28	N	N	
223	12	5-2-28	10-13-28	N	N	
234	13	5-3-28	10-13-28	N	N	
246	28	5-5-28	10-13-28	N	N	
247	29	5-6-28	10-13-28	N	N	
248	29	5-6-28	10-13-28	N	N	
249	29	5-6-28	10-13-28	N	N	
249	29	5-6-28	10-13-28	N	N	
250	30	5-7-28	10-13-28	N	N	
256	30	5-7-28	10-13-28	N	N	
257	32	5-7-28	10-13-28	N	N	
258	32	5-7-28	10-13-28	N	N	
260	32	5-9-28	10-13-28	N	N	
267	33	5-10-28	10-13-28	N	N	
268	33	5-10-28	10-13-28	N	N	
269	33	5-10-28	10-13-28	N	N	
270	34	5-11-28	10-13-28	N	N	
277	34	5-11-28	10-13-28	N	N	
278	37	5-14-28	10-13-28	N	N	
279	37	5-14-28	10-13-28	N	N	
280	47	5-16-28	10-13-28	Body	N	Body contains no germ cells; uterus slightly vascular.
288	45	5-16-28	10-13-28	N	N	
289	48	5-16-28	10-13-28	N	Body	Body contains no germ cells; uterus slightly vascular.
290	48	5-16-28	10-13-28	N	N	
299	38	5-16-28	11-1-28	N	N	
299	38	5-16-28	11-1-28	N	N	
334	38	5-16-28	11-1-28	N	N	

TABLE 2—*Concluded*

FEMALE NO.	AGE AT OPERATION IN DAYS	DATE OF OPERATION	DATE OF AUTOPSY	AUTOPSY FINDINGS		REMARKS
				Site right ovary	Site left ovary	
White 2457	15	5-16-28	11- 1-28	N	N	
458	15	5-16-28	11- 1-28	N	N	
459	15	5-16-28	11- 1-28	N	N	
460	15	5-16-28	11- 1-28	N	N	
Hooded 260	22	5-16-28	11- 1-28	N	N	
267	22	5-16-28	11- 1-28	N	N	
268	22	5-16-28	11- 1-28	N	N	
269	23	5-17-28	11- 1-28	N	N	
270	23	5-17-28	11- 1-28	N	N	
277	23	5-17-28	11- 1-28	N	N	
278	23	5-17-28	11- 1-28	N	N	
279	23	5-17-28	11- 1-28	N	N	
280	21	5-22-28	11- 1-28	N	N	
299	21	5-22-28	11- 1-28	N	N	
347	21	5-22-28	11- 1-28	N	N	
348	21	5-22-28	11- 1-28	N	N	
245	22	5-22-28	11- 1-28	N	N	
246	22	5-22-28	11- 1-28	N	N	

observation which perhaps substantiates the conclusion of Parkes ('26, '27) that neither the Graafian follicle nor the corpus luteum is necessary for the maintenance of uterine tone. The correlation between the occurrence of a capsule filled with a fluid or with blood and the vascularity of the uterus suggests the presence of a hormone (perhaps from interstitial tissue) which maintains the condition of the genital organs.

Preliminary reports of the first series were made in 1927 (also 1927b published 1929) and a general statement of the results of both series in 1929. Table 1 gives the operative history of the animals of the first series.

The influence of age on regeneration

The fact that no rats of the first series under forty days of age showed regeneration suggested that there is a correlation between the possibility of regeneration and the age of the animal at the time of operation, and that the younger the

animal when spayed, the less likelihood of regeneration. From a study of the first series it seemed that the chance of success in complete removal of the ovary increased as the age of the animal decreased.

With these facts in mind a second series, comprising rats under forty days of age (range ten to forty days) was initiated. One-hundred-eight rats were operated. Both ovaries were removed. The operative technique was identical with that employed in the first series. As a check on those under forty days of age, a few operations were performed on rats over forty days of age. Twenty-three of the 108 ranged in age from forty to fifty days. In all except three of this series the autopsy findings were entirely negative, the uterus in each case being very small and anemic. No trace of regenerated tissue was present. In each of three operated animals (age forty-seven to fifty days) a small body was present at the site of one excised ovary, the other site being negative. It is interesting to note that these

three were among the older rats operated as a check on the younger ones, so that in this series, as well as the first, no rats under forty days of age showed regeneration. Table 2 gives the operative history of the rats of the second series. In the three showing regenerated tissue the uterus at autopsy was vascular. The three regenerated masses, which were studied histologically and carefully examined for follicles, consist of small amounts of interstitial tissue, fibrous tissue, and fat, and show no cells resembling germ cells. The second series of operations is thus one hundred per cent negative.

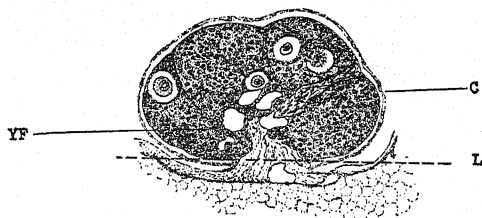


FIG. 18. SECTION THROUGH OVARY OF YOUNG RAT SHOWING SMALL, COMPACT OVARY

YF—young follicles. C—ovarian capsule. L—line of excision.

It seems to follow from these observations that the success of complete extirpation depends primarily on the age of the animal at the time of operation. The immature ovary of young rats is a small, ovoid body, freely movable, and not yet embedded in fat. When the thin capsule is slit by means of sharp scissors, the small, compact ovary "pops out" of the capsule. It can be cut off at the hilus easily and quickly. There is no bleeding from small capillaries to obscure the picture, since the characteristic vascularity of the region has not yet developed. In older rats, occasionally just beyond fifty days, and especially after maturity (about sixty-five days) the ovary is surrounded by fat and is very irregular in shape, owing to the presence of numerous follicles and

corpora lutea at or near the surface. In a number of instances a large lobe of the ovary was buried under the anterior end of the coiled tube. Such a lobe is easily overlooked at operation. Some bleeding from small vessels is always to be expected in the adult rat, notwithstanding all precautions to prevent it. This obscures the region somewhat, and makes complete removal of the lobed body difficult. In the two cases in the first series in which incomplete removal was demonstrated by

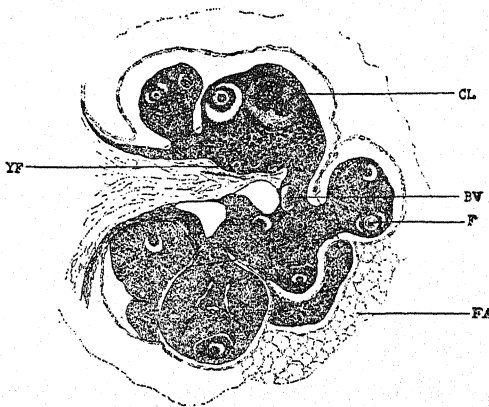


FIG. 19. SECTION THROUGH THE OVARY OF MATURE RAT, SHOWING THE LOBED CONDITION

Dotted lines indicate points at which a lobe might be cut off and left in place at excision. Sectioning in these planes might not reveal the absence of the lobe from the excised ovary. YF—young follicles. F—follicle. FA—fatty tissue.

sectioning the excised ovary, this was apparently the explanation. In both cases hypertrophy of the remaining piece followed, and young were subsequently born to both females.

From a study of variation in the shape of the mature ovary it seems that in some cases a lobe of the ovary may be almost constricted off from the rest. Several such cases came to light during the course of these experiments. In some instances this constriction was deep enough so that if the ovary were cut at this point, it could not be detected by sectioning the excised

piece. Thus a considerable amount of ovarian tissue might remain behind at operation, and, if the ovary were sectioned in the plane of the constriction, a study of the sectioned ovary might not reveal its absence. Large adult ovaries were sectioned in different planes to test such a possibility. There is evidence that this is the explanation in the cases of the first series where the excised ovary appeared complete, and yet regeneration occurred. In young rats such a difficulty is eliminated.

In the second series no regeneration occurred from 216 possible regeneration sites. It seems from these experiments that the *age factor* is the *determining factor* and that the operator can be certain of complete removal only in young rats. Such a conclusion is just the reverse of the observations of Davenport ('25), who found that throughout the experiment the age of the animal had no very definite effect, but that in some cases regeneration rates for mice between nine and ten weeks of age were relatively low, while others at four weeks gave as high as eighty-three per cent.

*Regeneration probably due to incomplete
removal of ovary*

When complete removal is possible, as in young animals, no regeneration follows, and it seems plausible to believe that the regeneration in older animals which occurred in these experiments, and perhaps those of other workers, was due wholly to the difficulties attendant upon a perfect ovariectomy.

It is a well-known fact of breeder's experience that castration in the male of fowls, horses, cattle, swine, etc., is not followed by regeneration of the testis. In the male the gonad is a discrete, freely movable body, and complete removal is

not difficult as it is with the lobed ovary of the female. The history of the human race supplies similar evidence. Castration was practised extensively in antiquity and still is practised in some oriental countries. So far as is known no cases in which normal male characteristics returned after early castration have ever been recorded.

Numerous instances are recorded in medical literature in which normal cyclic function was re-established and pregnancy subsequently occurred in women after removal of both ovaries. Clinical cases of this kind have been reported by Robertson ('90), Gordon ('96), Sutton ('96), Morris ('01), Doran ('02), Kynoch ('02), Meredith ('04) and others. In each instance the return of menstruation and the occurrence of pregnancy were attributed to incomplete removal at the time of operation. Meredith ('04) indicates the great possibility of incomplete ovariectomy even when care is taken to secure complete extirpation. He says (p. 1361):

In my own cases, the re-establishment of menstruation followed by pregnancy, is, of course, to be explained only by the theory that some portion of ovarian tissue capable of maturing follicles was left untouched by the operation, and further that the potency of one or other Fallopian tube was subsequently restored. The possibility of this occurrence has been fully established and need not, therefore, be discussed. On the other hand, the question of the probable site of the oöphoric tissue which escaped removal requires some brief consideration.

He refers to the possible existence of a third ovary, the occurrence of which had been previously described by some German gynecologists, but considers such an occurrence highly improbable. He explains his own cases as a question of an outlying portion of ovarian tissue in connection with the uterine extremity of one of the ovarian ligaments. Such a condition has been observed clinically and recorded in the literature.

SUMMARY

A general survey of the literature reveals four groups into which contributions dealing with the origin and history of definitive germ cells may be divided.

I. Those who deny early segregation of germ cells and believe that germ-cell formation is a matter of the differentiation of somatic cells.

II. Those who admit early segregation of germ cells, but conclude that such cells are not definitive and degenerate, to be replaced by proliferations of new cells from the epithelium.

III. Those whose investigations have led to the conclusion that germ cells are segregated early and migrate to the site of the developing gonad to persist as definitive ova or sperm, but that their numbers are increased periodically by proliferations from the epithelium.

IV. Those who believe that the definitive germ cells are set aside at an early stage in embryonic development, not to be replaced later by transformations of differentiated peritoneal cells. Their numbers are increased only by mitotic divisions.

The approach made from the standpoint of the regeneration of the gonad following removal throws light upon the problem of the definitive germ cells. If after extirpation of all gonadial tissue, the gonad is

even partially replaced by peritoneal proliferation, certainly this is evidence of the transformation of soma cells into germ cells. And if under optimum conditions gonadial tissue does not reappear, it is safe to conclude that soma cells do not proliferate germ cells.

The writer's experiments seem to show that it is easily possible to be certain of complete removal of the ovary in young rats (under forty days); and that upon complete removal no regeneration occurs. It seems logical to believe that the regeneration in older animals in these experiments was due to the difficulties inherent in a perfect ovariectomy. Thus the age factor becomes the determining factor. In operations performed on very young rats, when the capsule as well as the stalk remained in place, ample opportunity was afforded for proliferation from the epithelium, if somatic tissue has the power to proliferate generative cells. If no regeneration occurs under these conditions, it follows that the epithelium cannot regenerate the excised ovarian tissue. Thus in so far as these experiments bear on the problem of the definitive germ cells, they lend no support to origin from a peritoneal source. There is still some evidence that Weismannian continuity may be a tenable hypothesis.

LIST OF LITERATURE

- ADAMS, A. E., and E. S. KIRKWOOD. 1928. The effects of gonadectomy in *Triturus viridescens*. *Anat. Rec.*, 41: p. 35. Abstract.
- ALLEN, B. M. 1906. The origin of sex cells in *Chrysemys*. *Anat. Anz.*, 29: 217-236.
- . 1907. An important period in the history of the sex cells of *Rana pipiens*. *Anat. Anz.*, 31: 339-347.
- . 1910. The origin of the sex cells of *Amia* and *Lepidosteus*. *Jour. Morphology*, 22: 1-36.
- . 1911. The origin of sex cells in *Necturus*. *Science, N.S.*, 33: 268-269.
- ALLEN, EDGAR. 1922. Oestrous cycle in the mouse. *Amer. Jour. Anat.*, 30: 297-372.
- . 1923. Ovogenesis during sexual maturity. *Amer. Jour. Anat.*, 31: 439-481.
- ARAI, HAYATO. 1920a. Post-natal development of the ovary in the white rat. *Amer. Jour. Anat.*, 27: 405-462.
- . 1920b. On the cause of the hypertrophy of the surviving ovary after semi-spaying and the number of ova in it. *Amer. Jour. Anat.*, 28: 59-79.
- BACHMAN, FREDA M. 1914. The migration of the

- germ cells in *Amiurus nebulosus*. *Biol. Bull.*, 26: 351-366.
- BEARD, J. 1900. The morphological continuity of the germ cells in *Raja batis*. *Anat. Anz.*, 18: 465-485.
- VON BERENBERG-GOSSLER, H. 1912. Die Urgeschlechtszellen des Hühnerembryos am 3. und 4. Brütungstage, mit besonderer Berücksichtigung der Kern- und Plasmastrukturen. *Arch. f. mikr. Anat.*, 81: 24-72.
- . 1914. Über Herkunft und Wesen der sogenannten primären Urgeschlechtszellen der Amnioten. *Anat. Anz.*, 47: 241-264.
- BOHI, U. 1904. Beiträge zur Entwicklungsgeschichte der Leibeshöhle und der Genitalanlage bei den Salmoniden. *Morph. Jahrb.*, 32: 505-586.
- BRAMBELL, F. W. R. 1927. The development and morphology of the gonads of the mouse. Part I. Morphogenesis of the indifferent gonad and of the ovary. *Proc. Roy. Soc.*, 101: 391-408.
- BRAMBELL, F. W. R., A. S. PARKES, and UNA FIELDING. 1927a. Changes in the ovary of the mouse following exposure to x-rays. Part I. Irradiation at three weeks old. *Proc. Roy. Soc.*, 101: 29-55.
- . 1927b. Changes in the ovary of the mouse following exposure to x-rays. Part II. Irradiation at or before birth. *Proc. Roy. Soc.*, 101: 95-114.
- BRAMBELL, F. W. R., UNA FIELDING, and A. S. PARKES. 1928. Changes in the ovary of the mouse following exposure to x-rays. Part IV. The corpus luteum in the sterilized ovary and some concluding statements. *Proc. Roy. Soc.*, 102: 385-396.
- BUTCHER, EARL O. 1927. The origin of the definitive ova in the white rat, *Mus norvegicus albinus*. *Anat. Rec.*, 37: 13-29.
- . 1928. Germ-cell origin in the lake lamprey, *Petromyzon marinus unicolor*. *Anat. Rec.*, 41: p. 78. Abstract.
- CASTLE, W. E., and J. C. PHILLIPS. 1911. On germinal transplantation in vertebrates. Carnegie Publication no. 144: 1-26.
- . 1913. Further experiments on ovarian transplantation in guinea pigs. *Science*, 38: 738-786.
- CHILD, C. M. 1906. The development of germ cells from differentiated somatic cells in *Moniezia*. *Anat. Anz.*, 29: 592-597.
- . 1915. Senescence and Rejuvenescence. Chicago.
- COWPERTHWAIT, MARIAN H. 1925. Observations on pre- and post-pubertal oögenesis in the white rat, *Mus norvegicus albinus*. *Amer. Jour. Anat.*, 36: 69-86.
- DANTSCHAKOFF, W. 1908. Entwicklung des Blutes bei den Vögeln. *Anat. Hefte*, 37: S. 471.
- DAVENPORT, C. B. 1925. Regeneration of ovaries in mice. *Jour. Exper. Zoology*, 42: 1-11.
- DODDS, G. S. 1910. Segregation of the germ cells of the teleost, *Lophius*. *Jour. Morph.*, 21: 563-595.
- DOMM, L. V. 1927. New experiments on ovariectomy and the problem of sex inversion in the fowl. *Jour. Exper. Zoology*, 48: p. 31.
- DONALDSON, HENRY H. 1915. The Rat. *Memoirs of the Wistar Institute of Anatomy and Biology*, no. 6.
- DORAN, M. A. 1902. Pregnancy after removal of both ovaries for cystic tumor. *Jour. Obstet. and Gynec. British Empire*, 2: 1-10.
- DUESBERG, J. 1908. Les divisions des spermatocytes chez le rat. *Arch. f. Zellforsch.*, 1: 399-449.
- DUSTIN, A. P. 1907. Recherches sur l'origine des gonocytes chez les amphibiens. *Arch. de Biol.*, 23: 411-522.
- EIGENMANN, C. H. 1891. On the precocious segregation of the sex cells in *Micrometrus aggratus*, Gibbons. *Jour. Morph.*, 5: 481-493.
- ESSENBERG, J. M. 1923. Sex-differentiation in the viviparous teleost, *Xiphophorus helleri*. *Biol. Bull.*, 45: p. 46.
- . 1926. Complete sex-reversal in the viviparous teleost, *Xiphophorus helleri*. *Biol. Bull.*, 51: 98-111.
- FELIX, W. 1912. Development of the urogenital organs. *Human Embryology*. Keibel and Mall, Philadelphia., 2: 752-975.
- FELL, H. B. 1923. Histological studies on the gonads of the fowl. I. Histological basis of sex-reversal. *British Jour. Exper. Biol.*, 1: p. 97.
- FIRKET, J. 1914. Recherches sur l'organogenèse des glandes sexuelles des oiseaux. *Anat. Anz.*, 46: p. 413.
- . 1920. On the origin of germ cells in higher vertebrates. *Anat. Rec.*, 18: 309-316.
- FUSS, A. 1911. Über extraregionäre Geschlechtszellen bei einem menschlichen Embryo von vier Wochen. *Anat. Anz.*, 39: 407-409.
- . 1913. Über die Geschlechtszellen des Menschen und der Säugetiere. *Arch. f. mikr. Anatomie*, 81: 1-23.
- GATENBY, J. B. 1916. The transition of peritoneal epithelial cells in some amphibian Anura, especially *Rana temporaria*. *Quart. Jour. Micr. Sc.*, 61: 275-300.
- GOETTE, A. 1907. Vergleichende Entwicklungsgeschichte der Geschlechtsindividuen der Hydropolypen. *Zeitschr. f. wiss. Zool.*, 87: 1-335.

- GOLDSMITH, J. B. 1928. The history of germ cells in the domestic fowl. *Jour. Morph. and Physiol.*, 46: 275-315.
- GORDON, S. C. 1896. Two pregnancies following removal of both ovaries and ligation of tubes. *Trans. Amer. Gynec. Soc.*, 21: 104-106.
- HANN, H. W. 1927. The history of the germ cells of *Cottus bairdii* Girard. *Jour. Morph. and Physiol.*, 43: 427-480.
- HANSON, FRANK BLAIR, and FLORENCE HEYS. 1927. On ovarian regeneration in the albino rat. *Proc. Soc. Exper. Biol. and Med.*, 25: 183-184.
- . 1927. *Idem*. *Proc. Tenth Inter. Congress Zool. Budapest, Part I.* p. 547.
- HARGITT, G. T. 1913. Germ cells of Coelenterates. I. *Campanularia flexuosa*. *Jour. Morph.*, 24: 383-420.
- . 1916. Germ cells of Coelenterates. II. *Clava leptostyla*. *Jour. Morph.*, 27: 85-98.
- . 1917. Germ cells of Coelenterates. III. *Aglaantha digitalis*. IV. *Hybocadon prolifer*. *Jour. Morph.*, 28: 593-642.
- . 1918. Germ cells of Coelenterates. V. *Eudendrium ramosum*. *Jour. Morph.*, 31: 1-24.
- . 1919. Germ cells of Coelenterates. VI. General considerations, discussion, conclusions. *Jour. Morph.*, 33: 1-60.
- . 1924. Germ cell origin in the adult salamander, *Diemyctylus viridescens*. *Jour. Morph. and Physiol.*, 39: 63-111.
- . 1925. The formation of the sex glands and germ cells of mammals. 1. The origin of the germ cells in the albino rat. *Jour. Morph. and Physiol.*, 40: 517-557.
- . 1926. The formation of the sex glands and germ cells of mammals. 2. The history of the male germ cells in the albino rat. *Jour. Morph. and Physiol.*, 42: 253-305.
- . 1929. The formation of the sex glands and the germ cells of mammals. 3. The history of the female germ cells in the albino rat to the time of maturity. Abstract no. 131, Wistar Inst. Bibliographic Service, Nov. 30, 1929.
- HARTMAN, C. G. 1925. Observations on the functional compensatory hypertrophy of the opossum ovary. *Amer. Jour. Anat.*, 35: 1-24.
- HATERIUS, H. O. 1927. An experimental study of ovarian regeneration in mice. *Proc. Soc. Exper. Biol. and Med.*, 24: 784-786.
- . 1928. An experimental study of ovarian regeneration in mice. *Physiol. Zool.*, 1: 45-54.
- HEGNER, R. W. 1909. The origin and early history of the germ cells in some Chrysomelid beetles. *Jour. Morph.*, 20: 231-296.
- . 1912. The history of the germ cells in the paedogenetic larva of *Miastor*. *Science*, 36: 124-126.
- HEGNER, R. W. 1914. *The Germ-cell Cycle in Animals*. Macmillan, New York.
- HEYS, FLORENCE. 1929. Does regeneration follow complete ovariectomy in the albino rat? *Science*, 70: 289-290.
- HOFFMANN, C. K. 1886. Zur Entwicklungsgeschichte der Urogenitalorgane bei den Anamnia. *Zeitschr. f. wiss. Zool.*, 44: 570-643.
- HUBER, G. CARL. 1915. The development of the albino rat, *Mus norvegicus albinus*. I. From the pronuclear stage to the stage of mesoderm anlage; end of the first to end of the ninth days. *Jour. Morph.*, 26: 247-358.
- HUMPHREY, R. R. 1925. The primordial germ cells of *Hemidactylium* and other Amphibia. *Jour. Morph. and Physiol.*, 41: 1-43.
- . 1927a. Extirpation of the primordial germ cells of *Amblystoma*; its effect upon the development of the gonad. *Jour. Exper. Zool.*, 49: 363-399.
- . 1927b. The fate of the primordial germ cells of *Amblystoma* in grafts implanted in the somatopleure of other embryos. *Anat. Rec.*, 35: 40-41. Abstract.
- . 1928. The developmental potencies of the intermediate mesoderm of *Amblystoma* when transplanted into ventrolateral sites in other embryos: the primordial germ cells of such grafts and their rôle in the development of a gonad. *Anat. Rec.*, 40: 67-101.
- . 1929a. The early history of the primordial germ cells in Urodeles: evidence from experimental studies. *Anat. Rec.*, 42: 301-313.
- . 1929b. Studies on sex-reversal in *Amblystoma*. II. Sex differentiation and modification following orthotopic implantation of a gonadic preprimordium. *Jour. Exper. Zool.*, 53: 171-221.
- JARVIS, MAY. 1908. The segregation of the germ cells of *Phrynosoma cornutum*. *Biol. Bull.*, 15: 119-126.
- JENKINSON, J. W. 1913. *Vertebrate Embryology*. Oxford.
- JORDON, H. E. 1917. Embryonic history of the germ cells of the loggerhead turtle, *Coretta coretta*. *Carnegie Inst. Pub.* no. 251, 313-344.
- KANEL, V. Y. 1901. Regeneration processes in the ovaries of rabbits (in Russian). Kieff: Mattisen.
- KING, HELEN DEAN. 1908. The oögenesis of *Bufo lentiginosus*. *Jour. Morph.*, 19: 369-438.
- KINGERY, H. M. 1917. Oögenesis in the white mouse. *Jour. Morph.*, 30: 261-316.

- KINGSBURY, B. F. 1913. The morphogenesis of the mammalian ovary: *Felis domestica*. Amer. Jour. Anat., 15: 345-379.
- . 1914. Interstitial cells of the mammalian ovary. Amer. Jour. Anat., 16: 59-96.
- KOHNO, S. 1925. Zur Kenntnis der Keimbahn des Menschen. Arch. f. Gynäk., 126: 310-326.
- KUSCHAKEWITSCH, S. 1910. Die Entwicklungsgeschichte der Keimdrüsen von *Rana esculenta*. Festschr. f. R. Hertwig, 2: 61-224.
- KYNOCH, J. A. C. 1902. Repeated ovariectomy. Jour. Obstet. and Gynec. British Emp., 2: 366-371.
- LIPSCHUTZ, A. 1925. Dynamics of ovarian hypertrophy under experimental conditions. British Jour. Exper. Biol., 2: 331-346.
- MACLEOD, JULES. 1880. Contribution à l'étude de la structure de l'ovaire des mammifères. Arch. de Biol., 1: 241-278.
- . 1881. Recherches sur la structure et le développement de l'appareil reproducteur femelle des Teleostéens. Arch. de Biol., 2: 497-532.
- MARSHALL, F. H. A., and W. A. JOLLY. 1908. On the results of heteroplastic ovarian transplantation as compared with those produced by transplantation in the same individual. Quart. Jour. Exper. Physiol., 1: 115-120.
- MCCOSH, GLADYS. 1928. Origin of germ cells in *Amblystoma maculatum*. Anat. Rec., 41: p. 78. Abstract.
- MEREDITH, W. A. 1904. Pregnancy after removal of both ovaries for dermoid tumor. British Med. Jour., 1: p. 1360.
- MIHALKOVICS, V. 1885. Untersuchung über die Entwicklung des Harn- und Geschlechtsapparates der Amnioten. Internat. Monat. Anat. und Histol., 2. Abstract.
- MINOT, C. S. 1894. Gegen das Gonatom. Anat. Anz., 9: 210-213.
- MONTGOMERY, T. H. 1906. The Analysis of Racial Descent in Animals. New York. Henry Holt and Co.
- MORGAN, T. H. 1901. Regeneration. New York. Macmillan Co.
- MORRIS, M. M. 1901. Pregnancy following removal of both ovaries and tubes. Boston Med. and Sur. Jour., 144: p. 86.
- NUSSBAUM, M. 1880. Zur Differenzierung des Geschlechts im Tierreich. Arch. f. mikr. Anat., 18: 1-121.
- OKKELBERG, P. 1921. The early history of germ cells in the brook lamprey, *Entosphenus wilderi* Gage, up to and including the period of sex differentiation. Jour. Morph., 35: 1-152.
- PALLOT, G. 1928. À propos de la régénération ovarienne et des modifications périodique de l'épithélium vaginal chez le rat blanc. C. R. de la Soc. de Biol., 99: 1333-1334.
- PAPANICOLAOU, G. N. 1925. Oögenesis during sexual maturity as elucidated by experimental methods. Soc. Exper. Biol. and Med., 21: p. 393.
- PARKES, A. S. 1926. On the occurrence of the oestrous cycle after x-ray sterilization. Part I. Irradiation at three weeks old. Proc. Roy. Soc., 100: 151-170.
- . 1927a. On the occurrence of the oestrous cycle after x-ray sterilization. Part II. Irradiation at or before birth. Proc. Roy. Soc., 101: 71-94, 95-114.
- . 1927b. On the occurrence of the oestrous cycle after x-ray sterilization. Part III. The periodicity of oestrus after sterilization of the adult. Proc. Roy. Soc., 101: 421-449.
- . 1927c. On the occurrence of the oestrous cycle after x-ray sterilization. Part IV. Irradiation of the adult during pregnancy and lactation; general summary. Proc. Roy. Soc., 102: 51-62.
- PARKES, A. S., and C. W. BELLERBY. 1926. Studies on the internal secretion of the ovary. Part I. The distribution in the ovary of the oestrus-producing hormone. Jour. of Physiol., 61: 562-575.
- PARKES, A. S., UNA FIELDING, and F. W. R. BRAMBELL. 1927. Ovarian regeneration in the mouse after complete double ovariectomy. Proc. Roy. Soc., 101: 328-354.
- PATTERSON, J. T. 1913. Polyembryonic development in *Tatusia novemcincta*. Jour. Morph., 24: 560-682.
- PENCHARZ, R. I. 1929a. Experiments concerning ovarian regeneration in the white rat and white mouse. Abstract no. 2322, Wistar Institute Biblio. Ser., July 31, 1929.
- . 1929b. *Idem*. Jour. Exper. Zool., 54: 319-339.
- RICHARDS, A., H. R. HULPIEU, and J. B. GOLDSMITH. 1926. A restudy of the germ-cell history in the fowl. Anat. Rec., 34: p. 158. Abstract.
- RICHARDS, A., and J. T. THOMPSON. 1921. The migration of the primary sex cells of *Fundulus heteroclitus*. Biol. Bull., 40: 325-348.
- ROBERTSON, J. A. 1890. Renewal of menstruation and subsequent pregnancy after removal of both ovaries. British Med. Jour. 2: p. 722.
- RUBASCHKIN, W. 1908. Zur Frage von der Entstehung der Keimzellen bei Säugetierembryonen. Anat. Anz., 32: 222-224.
- . 1910. Über das erste Auftreten und Migra-

- tion der Keimzellen bei Säugetierembryonen. Anat. Hefte, 41: p. 243.
- SCHULTZ, W. 1900. Transplantation der Ovarien auf männliche Tiere. Zentralbl. f. allg. Path., 2: 200-202.
- SIMKINS, C. S. 1923. Origin and migration of the so-called primordial germ cells in the mouse and rat. Acta Zoologica, 4: 241-278.
- . 1928. Origin of sex cells in man. Amer. Jour. Anat., 41: 249-272.
- SOLNAKER, J. R. 1927. Semi-ovariectomy hypertrophy of the remaining ovary and migration of ova in the albino rat. Amer. Jour. Physiol., 81: 620-627.
- STROMSTEN, F. A. 1929. History of the germ cells in the goldfish. Anat. Rec., 44: p. 254. Abstract.
- SUTTON, R. S. 1896. Double ovariectomy followed by pregnancy and delivery at term. Trans. Amer. Gynec. Soc., 21: 109-110.
- SWEZY, OLIVE. 1929a. Maturation of the male germ cells in the rat. Abstract no. 2334, Wistar Inst. Biblio. Ser., Aug. 15, 1929.
- . 1929b. The ovarian cycle in a mixed rat strain. Abstract no. 2335, Wistar Inst. Biblio. Ser., Aug. 15, 1929.
- SWEZY, OLIVE, and H. M. EVANS. 1929a. Maturation of human embryonic ova. Proc. Soc. Exper. Bio. and Med., 27: p. 10.
- . 1929b. Ovogenesis in the mammals. Proc. Soc. Exper. Biol. and Med., 27: p. 11.
- SWIFT, C. H. 1914. Origin and early history of primordial germ cells in the chick. Amer. Jour. Anat., 15: 483-516.
- . 1915. Origin of the definitive sex cells in the female chick, and their relation to the primordial germ cells. Amer. Jour. Anat., 18: 441-470.
- . 1916. Origin of sex-cords and definitive spermatogonia in the male chick. Amer. Jour. Anat., 20: 375-410.
- SWINGLE, W. W. 1921. The germ cells of Anurans. I. The male sexual cycle of *Rana catesbeiana* larvae. Jour. Exper. Zool., 32: 235-301.
- . 1926. The germ cells of Anurans. II. An embryological study of sex differentiation in *Rana catesbeiana*. Jour. Morph. and Physiol., 41: 441-516.
- TAMURA, Y. 1926. The effects of implantation upon ovarian grafts in the male mouse. Proc. Roy. Soc. of Edinburgh, 47: 148-164.
- TSCHASCHIN, S. 1910. Über die Chondriosomen der Urgeschlechtszellen bei Vögelembryonen. Anat. Anz., 37: 597-607, 621-631.
- VANNEMAN, A. S. 1917. The early history of the germ cells in the armadillo, *Tatusia novemcincta*. Amer. Jour. Anat., 22: 341-364.
- Voss, H. E. V. 1925. Condition de la greffe ovarienne intratesticulaire. Comptes Rendues Soc. de Biol., 93: 1066-1071.
- WALDEYER, W. 1870. Eierstock und Ei. Leipzig.
- WEISMANN, AUGUST. 1883. Entstehung der Sexualzellen bei den Hydromedusen. Jena.
- . 1904. Vorträge über Descendenztheorie. English Translation. London. Two volumes.
- WILLIER, B. H. 1926. The development of implanted chick embryos following the removal of the 'primordial germ cells.' Anat. Rec., 34: p. 158. Abstract.
- WILSON, H. V. 1913. Heredity and microscopical research. Science, N.S., 37: 814-826.
- DE WINIWARDER, H. 1910. Contribution à l'étude de l'ovaire humain. I. Appareil nerveux et phéochrome; II. Tissue musculaire; III. Cordons médullaires et corticaux. Arch. de Biol., 25: 683-756.
- DE WINIWARDER, H., and G. SAINMONT. 1909. Nouvelles recherches sur l'ovogenèse et l'organogenèse de l'ovaire des mammifères (chat). Arch. de Biol., 24: 1-142, 165-276, 373-431, 628-650.
- WOLF, L. E. 1929. Transformation of epithelial cells into germ cells in *Platyopocilus maculatus*. Anat. Rec., 44: p. 261. Abstract.
- WOODS, F. A. 1902. Origin and migration of germ cells in *Acanthias*. Amer. Jour. Anat., 1: 307-320.
- WOODS, F. H. 1925. History of the germ cells in *Sphaerium striatinum*. Anat. Rec., 31: p. 305. Abstract.
- . 1929. History of the germ cells in *Sphaerium striatinum*. Anat. Rec., 44: p. 230. Abstract.

The following contributions were not available. They are mentioned here for the sake of completeness.

- ANCEL, P., et P. BOUIN. 1926. Recherches expérimentales sur l'origine des gonocytes dans le testicule des mammifères. C. R. Ass. Anat., 21.
- BOVERI, T. 1892. Die Entstehung des Gegensatzes zwischen den Geschlechtszellen und den somatischen Zellen bei *Ascaris megalocephala*. Sitz. Ges. f. Morph. Phys. München, 8.
- JANDA, VIKTOR. Title not known. A study of regeneration after excision of the ninth to twelfth segments in *Stylaria lacustris*. Jahrb. Abt. Allg. Zool. u. Physiol., 43: 339-360.
- PARKES, A. S., F. W. R. BRAMBELL, and UNA FIELDING. 1927. Effect of x-rays on the ovary of the mouse. C. R. Ass. Anat., 22.
- TRUFFI, G. 1926. Sur la régénération de l'ovaire. C. R. Ass. Anat., 21.



THE RÔLE OF BACTERIA IN THE NUTRITION OF PROTOZOA

By J. MURRAY LUCK, GRACE SHEETS, AND JOHN O. THOMAS
Laboratory of Chemophysical Biology, Stanford University, California

*Contribution No. 1 of "Studies on Protozoa" by H. Clark, J. M. Luck, and C. V. Taylor.
Presented before the Western Society of Naturalists, at the Eugene meeting of
the Pacific Division, A. A. A. S., Eugene, Oregon, June 18-21, 1930*

INTRODUCTION

ACCORDING to Calkins (1) four principal types of nutrition are to be found among the protozoa. Some are holozoic or holophytic, dependent for maintenance upon other living organisms as sources of food. Others have developed a saprozoic or saprophytic mode of nutrition and are able to live on dead organisms or the products of their disintegration. A third group is autotrophic. The presence of a photosynthetic pigment permits the organism to utilize the energy of sunlight in the elaboration of complex tissue constituents from the simplest of raw materials. Finally there are heterotrophic protozoa which are able, as has been fairly well demonstrated, to live both saprophytic and autotrophic modes of existence. Many colored flagellates are autotrophic in light and saprophytic in the dark. In fact the saprophytic flagellates are conceivably derived from heterotrophs by loss of the photosynthetic pigment.

In this paper we propose to confine our attention to nutrition of the first two types and, in particular, we shall enquire into that knotty problem of forcing a normally holozoic animal to lead a saprophytic existence. Our purpose in so doing is not only to attempt the teaching of new

tricks to the protozoa. Nor do we care merely to assist in unravelling the threads of inter-related fact that are so confusingly tangled in the baffling problems of holozoic nutrition, even though a satisfying explanation of these phenomena would constitute one of the most fundamental contributions to our knowledge of nutrition. Rather, we have found ourselves lured on by an objective of different and perhaps more immediate consequence. It is our intention to study the chemistry of protozoan metabolism, the nature and significance of those elementary and molecular constituents of protoplasm, which though present in very small quantities are nevertheless indispensable for the maintenance and well-being of the organism, the nature and mode of action of toxic agents, the effects of radiation of high intensity, in short a number of problems which demand that the protozoon under investigation be unaccompanied by other living forms. If a normally holozoic organism is to be studied along these lines it is apparent that the creature must, if possible, be led into the ways of its saprophytic cousins.

Specificity in selection of food

One of the first considerations of great importance is the surprising measure of specificity that normally prevails among

the holozoic feeders. Thus we are reminded that the holotrich *Actinobolus radians* prefers to dine only on *Halteria*, while the active ciliate *Didinium nasutum* concentrates its predatory attacks on *Paramecium*. Incidentally their exploits in food-getting are full of thrills. In the words of Calkins (2) "next to the capture of *Halteria grandinella* by *Actinobolus radians* I know of nothing more spectacular or amazing in the whole realm of microscopy than the seizure and ingestion of *Paramecium* by *Didinium*." The Suctorians seem to relish certain of the ciliates, other protozoa ingest principally a given flagellate, and so the specialization continues. [The co-existence of paramoecia and unicellular algae appears to be true symbiosis, rather than a selective digestion of algae as food by *Paramecium* (3, 4).] Indeed the work of Lund (5), Mast, Schaeffer, and others indicates that discrimination in the selection of food is general among the infusoria.

Among the bacteria-eaters the same selectivity is to be found. In 1897 Frosch (6), who succeeded in culturing *Amoeba nitrophila*, a soil form, on pure lines of bacteria, observed that several were totally unsatisfactory as food for the amoeba, others were fair, and one proved to be excellent. For twenty years, the admirable pioneer work of Frosch, Tsujitani (7), Beijerinck (8) and Mouton (9) in this difficult field was almost completely overlooked or ignored. The exhaustive work of Musgrave and Clegg (10) is an outstanding exception. Though it was realized quite well that the bacterial flora of the infusions used in culturing protozoa was the most important variable, few serious attempts were made to control it. In the words of Hargitt and Fray (11) (describing the cultivation of *Paramecium* in hay infusions), "it is rather striking that not a single effort has been

made by modern methods to analyze the hay infusion bacteriologically." In 1917, however, Hargitt and Fray (11) plated out the bacteria from normal and abnormal hay infusions. Examination of the dominant strains showed that eight or more used singly as food for bacterial-free *Paramecium* (*aurelia* and *caudatum*) were quite unsatisfactory. The division rate relative to that obtaining in a mixed bacterial flora was markedly depressed. Extinction of the protozoon line followed within twelve days. Only one strain seemed promising. On *B. subtilis* the division rate over a fifteen day period was 1.31 compared with 1.14 in the reference mixed culture. However, the *B. subtilis* experiments were few in number and of short duration. "It seems clear" concluded Hargitt and Fray "that cultures of mixed bacteria are, as a rule, far superior as a diet for *Paramecium* to any one kind of bacteria. . . . It should be possible" they add "by using cultures of bacteria, mixing these known forms in various combinations in sterile infusions and growing *Paramecium* therein to secure a mixture which would be better than the ordinary mixed cultures" Calkins (12) seems to have held the opinion that *B. subtilis* was probably the principal food of *Paramecium* in hay infusions. The work of Musgrave and Clegg (10) demonstrated striking selectivity in the utilization of bacteria as food by the amoebae. Undoubtedly the most extensive inquiry into the discriminations that prevail among the protozoa in the choice of food has been pursued by Oehler of Frankfurt (13-17). A series of papers published between 1916 and 1924 reveal some surprising differences in holozoic nutrition among the protozoa. "Wenn man in dieser Weise, Amöben auf eine Bakterienrein-kultur zu überführen sucht, so zeigen sich

merkliche Unterschiede. Bei manchen Bakterien gelingt die Überführung leicht, bei anderen schwer oder gar nicht." (13). Among the amoebae it was found that *Hartmanella aquarum* and *Vahlkampfia magna* would assimilate any of the bacteria tried except the timothy bacillus. *B. bulgaricum* and a certain soil staphylococcus were also not acceptable. But yeast (*Saccharomyces exiguus*) and several small amoebae were ingested. In addition it was observed that all five amoebae preferred gram-negative bacteria to gram-positive forms. Bacteria from young cultures were found better than those from old. Some rather resistant strains proved to be edible if eaten young. Bacterial spores, mold mycelia and spores, unicellular algae, and diatoms were refused by all five amoebae. Flagellates and ciliates, so Oehler reported (14), would live equally well on gram-negative and gram-positive bacteria. The timothy bacillus, though refused by amoebae, was accepted by the flagellates and ciliates. The former would eat all bacteria examined but not the yeast, *Saccharomyces exiguus*, which was probably too large. The ciliate *Colpoda Steini* would digest both yeast and mold spores. Phillips (18) reported the interesting observation that *Paramoecium aurelia*, which grew fairly well on her C' strain of bacteria with a division rate of 1.03 over a seven month period, showed an enhanced rate of reproduction of 1.79 on the mixture A' and C'; this despite the fact that A' alone was incapable of supporting the growth of *Paramoecium*. C' was a streptothrix. Nine other pure lines of bacteria were examined but, singly or in the twelve combinations tried, they failed to suffice. Cutler and Crump (19) have also investigated the nutritive value of different strains of bacteria in the maintenance of *Hartmanella*. They were able to show

that the poor nutritive quality of two species of bacteria used by them was not due to the formation of toxic products. In some instances it is doubtless true that the failure of a protozoon to feed on a given bacterium is due to the formation of carbon dioxide, ammonia, trimethylamine, or other noxious substance as a product of bacterial metabolism (13). It is of interest in this connection that the diphtheria toxin liberated in a culture of diphtheria bacillus is apparently innocuous to three ciliates studied by Oehler (16). The inadequacy of a given bacterial species for protozoon nutrition may in some instances be due to the establishment of an unfavorable hydrogen ion concentration in the medium in consequence of bacterial growth. In other cases the size or shape of the bacteria may be unfavorable. It is also possible that the protozoon requires certain accessory food factors which are not to be found in all bacteria. Finally it is conceivable that the protozoon is unable to elaborate its protoplasmic constituents from the fairly simple substances utilized by the higher animals. The assimilation, without preliminary hydrolysis and subsequent formation, of highly organized substances may be necessary in this group. If so there is the possibility that these complex nutrients are of limited occurrence among the bacteria. Certainly, the presence of proteolytic enzymes in protozoon extracts (9) cannot be considered proof that proteolysis precedes the utilization of ingested protein. Most recently, Cleveland and Sanders (20) have reported definite selectivity in the utilization of bacteria by *Entamoeba histolytica*.

The technique of sterilizing protozoa

A second consideration of great importance is that of rendering protozoa bacterial-free, for only after securing a

sterile strain can one investigate the conditions of saprophytic growth on synthetic media. Four principal methods have been employed, sterilization of cysts, washing, negative geotaxis, and cataphoresis. The last of these was introduced by Amster (21), who succeeded in freeing ciliates of bacteria by inserting non-polarizable electrodes in the suspension of organisms. 0.05 per cent sodium chloride was added for conductivity. The ciliates moved to the cathode and the bacteria to the anode. Six repetitions were sufficient to sterilize the protozoa. It seems improbable that this method of sterilization would be of general utility and applicable to all bacteria. The electrical charge possessed by bacteria varies with species and hydrogen ion concentration (22) (23). Amster studied the ciliate *Balantiophorus* which he cultivated, uncontaminated with foreign bacteria, on a single but unidentified species in 0.1 per cent Witte peptone. The method of negative geotaxis seems to have had a limited trial among a few workers. It takes advantage of the fact that some protozoa when confined in a tube of media cluster about the surface. The accompanying bacteria, meanwhile, disperse themselves throughout the fluid. It is assumed therefore that after many serial transfers of the surface portions to fresh tubes of sterile media, the bacteria will be diluted out. This method has never received a satisfactory critical study. Washing of the protozoa in sterile water seems to have been employed the most. Hargitt and Fray (11) washed the protozoa free of bacteria by running them one at a time through five portions of sterile wash fluid in covered depression slides. The transfers were made with sterile micro pipettes. The final wash fluid and the fully bathed animals are said to have been sterile. Peters (24) used

essentially the same procedure but limited his sterility tests to the final wash fluid. Phillips (18) modified the procedure slightly but seldom tested the washed protozoa for sterility. This omission served as the basis of Parpart's criticism (25) and led to the recommendation of another simple but important modification. Parpart found that five washings, 8 animals at a time, gave a sterile final wash fluid but even after 10 washings in 6 out of 8 trials the animals themselves were infected. Acting on the assumption that *Paramoecium* had ingested bacterial spores which therefore escaped removal by the washing process, Parpart halted the procedure while the animals were in the fifth wash fluid for 5 hours. This provided time for the defecation of spores. Four final washings then followed. The resultant animals were sterile. Still another method, one which found particular favor among the earlier workers, was that of Frosch (6). It consisted in sterilization of the protozoan cysts. Frosch sterilized old cysts of *Amoeba nitrophila* by immersion in saturated sodium carbonate at room temperature for 3 days. Young cysts were not sufficiently resistant for this drastic treatment. Non-sporulating bacteria were killed. Concentrated sodium chloride and sucrose were also of value. More recently, Severtzoff (26) has reported success in sterilizing amoeba cysts with toluene, chlorine, and calcium sulphide. Tsujitani (7) resorted to desiccation of the cysts, while Walker (27) observed that moist heat at 70°-75° for 1 hour was sufficient to kill non-sporulating organisms without injury to amoeba cysts. Oehler (17) found that long heating of the cysts (six weeks at 37° or several hours at 60°-64°) was successful. These observations are in need of confirmation. Oehler contended

that it is almost impossible to free ciliates of bacteria by washing.

If merely a mono-bacterial strain of a protozoon is desired, two methods have been reported satisfactory. The first, that of Beijerinck (8), is the oldest in protozoology. It has been of particular service in studies upon amoebae, though other protozoa may be employed. It consists in streaking agar plates radially or by a central circular smear with the strain of bacteria upon which the protozoon is to be nourished. The center of the plate is then inoculated with amoebae from the stock mixed culture. The amoebae feed upon the new bacteria and travel towards the periphery leaving the old contaminants behind them. By this means Beijerinck developed pure lines of *Amoeba nitrophila* and *Amoeba zymophila* on acetic acid bacteria, *Saccharomyces apiculatus*, and *B. coli communis*. Tsujitani (7) grew three kinds of amoebae in mono-bacterial culture on cholera bacilli, typhus bacilli, *B. coli communis*, *B. fluorescens*, *Staphylococcus pyogenes aureus*, *B. pyocyaneus*, *B. ruber*, and three or four other forms. Mouton (9) secured a fine culture of an amoeba on *B. coli communis*. Other bacteria were less satisfactory and *B. anthracis* was poor. A second procedure developed by Oehler (14, 17) consisted in replacing one bacterial strain by another through change of medium. Thus *Colpidium colpoda*, contaminated with several species of bacteria, was added to a pure culture of hay bacillus in 1 to 2 per cent peptone. The other bacilli associated with *Colpidium* were suppressed, leaving the hay bacillus. The addition of sterile urine and inoculation with *B. prodigiosus* caused the suppression of all bacteria but the latter, so Oehler reports. There resulted a pure line of *Colpidium* on *B. prodigiosus*. Likewise the use of a sugar-peptone medium permitted replacement by *B. coli*

communis. Complete sterilization of *Colpidium* was never accomplished by Oehler. In our own experiments with the hypotrich *Euplotes taylori* we found that success in sterilization by washing was largely dependent on the quantity of bacteria. The time spent in the various baths is also an important factor.

Attempts to rear protozoa saprophytically

Of great significance are the attempts which have been made to rear protozoa saprophytically. Tsujitani (7) appears to have been the first to study saprophytic nutrition in the protozoa, although it should be mentioned that Kartulis (28) some years before reported that liver abscesses containing the dysenteric amoeba had been found by him to be free of bacteria. Cleveland and Sanders (20) have recently succeeded in producing bacteria-free amoebic abscesses in the livers of cats. In vitro, they were unable to cultivate the amoeba (*E. histolytica*) in the absence of living bacteria. From a hay infusion Tsujitani isolated a non-sporulating bacterium, which though heated to 60°-70° for 40 minutes would still serve as food for amoebae. Frosch (6), on the contrary, was unsuccessful in growing his amoeba on dead bacteria or on digests or extracts of bacteria. Musgrave and Clegg (10), likewise, were of the opinion that other living organisms were indispensable for the nourishment of amoebae. Frosch concluded that the amoeba was not a saprophyte "sondern ein Lebewesen, das zu seiner Ernährung bestimmter lebender Elemente benötigt, die anscheinend nur im lebenden Organismus vorhanden sind." The same opinion was expressed by Casagrandi and Barbagallo (29): "Man kann wohl sagen, dass es unmöglich ist, eine Amöbenkultur zu haben, ohne dass man zu gleicher Zeit sich Bakterien darin entwickeln sieht."

Tsujitani's observations remained unconfirmed for nearly 20 years. In 1911, Wülker (30) in his excellent review on amoeba culture, felt constrained to point out that "eine genaue Nachprüfung dieser bis jetzt unbestätigten Versuche ist sehr erwünscht." In 1916, Oehler reported the first of his observations which served to confirm and greatly extend the work of Tsujitani. Oehler found (13) that sterile *Hartmanella* and *Vahlkampfia* would eat and digest all bacteria, killed at 100°, which were examined. Three other sterile strains of amoebae could not be so maintained. Of the latter, however, one would ingest bacteria killed by heating at 56° for 1½ hours. The second could be maintained on *B. fluorescens* if killed at 45° for 1½ hours, but the third refused all "cooked" food. Heat-killed coli, cholera vibrios, proteus, fluorescens, sarcina, and yeast were used in these experiments. Among the ciliates, Oehler found (14) that the small forms seemed most adaptable to a diet of dead bacteria. *Colpoda Steini*, sterilized after great difficulty, would live and multiply on *B. coli* heated to 100° for 1 hour or 56° for 1½ hours. Heated yeast and heat sterilized suspensions of finely powdered casein, edestin, and muscle powder were also adequate for nutrition of *Colpoda Steini* and the flagellate *Prowazekia*. Heated blood serum (64°–74°) was found to be a good sterile food for sterile amoebae (17). Curiously enough, boiled spinach was excellent. Bacteria killed with ether or acetone were seldom satisfactory. Fat droplets, red blood cells, fibrin, starch grains, milk, and egg yolk were never adequate (13). All experiments with soluble foodstuffs were unsuccessful (31). Peters (24), on the contrary, reported excellent results in the cultivation of sterile *Colpidium colpoda* on a very simple synthetic medium of soluble constituents.

The organic compounds employed in the first medium were merely three amino acids, glucose, and ammonium lactate. In other experiments ammonium glycerophosphate was found to be sufficient. The ciliate multiplied to over 10,000/cc. The organisms were sterilized by washing. Several, being unsuccessful in similar attempts, have insisted that Peters' sterility tests were not sufficient. It is contended that bacteria were present upon which *Colpidium* fed. Incidentally, Oehler never succeeded in maintaining *Colpidium colpoda* on anything but live bacteria (15). (Since this paper was submitted for publication, others in this University and ourselves have succeeded in cultivating *Colpidium colpoda* in bacteria-free media.)

Quantity of food

Several miscellaneous factors, of importance in the nutrition of protozoa, remain to be disposed of before passing on to the experimental portion. One of these, carefully investigated by Cutler and Crump, is that of the quantity and quality of food. We have already considered the latter at some length except for one phase to which Cutler and Crump in particular made a valuable contribution (32). They devoted themselves to a study of the effect of age on the reproductive rate. Working with *Colpidium colpoda* and *Oicomonas termo* they found that the division rate of organisms from a 24 hour parent cell community was much higher than that of organisms taken from a culture 4 or 5 days old. They used a simple synthetic basal medium. *Oicomonas* was fed on 3 or more strains of bacteria contained therein. *Colpidium* was associated with a stout bacillus and in addition was fed with *Sarcina lutea*. Accordingly there was not a rigorous control of the bacterial flora. Likewise Robertson (33) observed

that a single *Enchelys* from a culture one day old multiplied to 38.4 in 24 hours. If the parent community was 2 days old, the multiplication was reduced to 5.9, if 3 days old, 2.6, and 4 days old, 2.0. In many instances the lowered fission rate is due to toxic metabolic products carried over from the old cell community. It is possible too that organisms from old cell communities are depleted of some essential growth principle. Thus Beers (34) has shown that starved paramoecia fed to *Didinium* result in the degeneration of the line as evidenced by decreased fission rate, increased death rate, and production of abnormal individuals. On the contrary the control line on well-fed paramoecia continued in a vigorous, flourishing state. Cutler and Crump also showed (19, 35) that the rate of division of protozoa is a function of the quantity of food. Thus a contaminated line of *Colpidium* fed with increasing proportions of *Sarcina lutea* showed the following striking changes in the division rate for 24 hour periods.

NUMBER OF BACTERIA PER COLPIDIUM	DIVISION RATE (AVERAGE)	NUMBER OF BACTERIA PER COLPIDIUM	DIVISION RATE (AVERAGE)
250	0.1	16000	0.7
500	0.1	32000	1.5
1000	0.3	64000	2.4
2000	0.3	128000	2.9
4000	0.3	256000	3.9
8000	0.4	512000	4.1
		1024000	5.3

Incidentally, removal or reduction in numbers of the contaminating bacillus from *Colpidium* caused degenerative changes.

Allelocatalysis

Reference has already been made to the possible existence of a growth-promoting principle in protozoa. This hypothesis

was first advanced by Robertson (33), who showed in the case of *Enchelys* that the initial lag phase was followed by a period in which there seemed to be a mutual acceleration of growth on the part of the protozoa. In any case the division rate of an organism contained in a small volume of medium was demonstrably greater than that of an organism contained in a large volume. Both organisms used in the inoculation were of course drawn from the same parent community. Robertson postulated the existence of a growth-promoting principle described as substance X which was considered to be of nuclear origin. It was liberated into the surrounding medium on cell division. With this assumption it follows at once that the concentration of X would be greater if the initial volume of medium be small than if it be large. As a corollary it is apparent that one important rôle of bacteria could be that of serving as a source of a similar X principle, in addition to the recognized function of serving as food. Robertson bolstered up his hypothesis and elevated it to the plane of sound theory by showing that growth-promoting principles could be extracted in crude form from yeast. He did not discuss the possibility, neither did Cutler and Crump (36), nor Gregory (37), that extracts of yeast, bacteria, protozoa, and bios preparations may exert their growth-promoting effect by serving as organic foodstuffs for the enrichment of the associated bacterial flora. The observation reported by Peters (24) that an isolated protozoon would not grow in 1 cc. of medium although 20 to 40 organisms would do so, has been confirmed by many. It obviously lends support to Robertson's theory of allelocatalysis. Likewise Yocom's observations (38) on *Oxytricha* fit in well with this hypothesis. Arrayed against it, however, are the findings of

Cutler and Crump (36) on *Colpidium colpoda*, Myers (39) on *Paramoecium caudatum*, of Greenleaf (40), Woodruff (41), and probably many others whose findings we have not recorded. There is great need for the re-investigation of this important problem under rigid bacteriological control.

EXPERIMENTAL

The Organism

The protozoon used in our investigations was the hypotrich, *Euplotes taylori*, first described by Garnjobst in 1926 (42). The organism is a marine form common in tide pools and brackish waters in the San Francisco bay region. It is of special interest because encystment, to which it is subject, may be induced experimentally. Excystment is also amenable to control. Salt concentration is one of the significant determining factors. This important phenomenon is now receiving extensive investigation.

In addition the organism is to be employed in a study of the effect of X-rays of great intensity, in the course of which the whole animal or parts thereof will be irradiated. Morphological and chemical changes resulting from this treatment will be investigated.

For the purposes of this investigation we have devoted ourselves for some months to experiments on the nutrition of *Euplotes taylori* with the object before us of cultivating the organism in a simple synthetic medium. In this paper we shall demonstrate that the basal medium may be of great simplicity and the bacterial flora amenable to rigid control. We have not yet achieved success in culturing the organism saprophytically although we do not consider the maintenance of the ciliate in a bacterial-free medium to be an unattainable goal.

Sterilization of Euplotes taylori

A satisfying inquiry into the nutrition of the protozoon presupposes that it may, for experimental purposes, be rendered free of bacteria. The method which we have ultimately found to be adequate is, in principle, that of Hargitt and Fray (11). The process consists in the transfer of 10 to 15 *Euplotes* through 10 to 15 sterile baths in series. As containers of the washing medium, we have employed small watch glasses, arranged in individual Petri dishes. The transfers are made with capillary pipettes drawn from #6 glass tubing to a length of about 10 cm. and to a distal diameter of about 0.3 mm. The opposite end of the pipette is plugged with cotton and inserted into a piece of rubber tubing about 30 cm. long. The application to this tube of suction by mouth permits a delicacy of control in operation of the pipette that we have been unable to duplicate with the usual rubber bulbs. A new pipette is used for each transfer. After use it is discarded permanently. During the transfer the cover of the Petri dish is raised just enough to permit insertion of the capillary portion of the pipette. A binocular dissecting microscope is essential.

All glassware is sterilized by heating to 170° for 2 hours. Aseptic precautions are necessarily employed throughout.

The washing medium, of which 2 cc. are placed in each watch glass, consists of sterile 1:1 artificial sea water. This is prepared according to the following formula which is based, in turn, upon the sea water analyses of Page (43) (Cf. also Harvey (44)).

	grams
Sodium chloride.....	26.10
Magnesium chloride ($MgCl_2 \cdot 6H_2O$).....	6.20
Magnesium sulphate ($MgSO_4 \cdot 7H_2O$).....	4.07
Calcium sulphate, anhydrous.....	1.15
Potassium chloride.....	0.60

Disodium hydrogen phosphate.....	0.01
Ferric chloride (FeCl ₃).....	0.01

Culturing Technique

The salts are dissolved in twice distilled water and the solution diluted to a volume of one liter. The artificial sea water thus obtained is diluted with an equal volume of distilled water and designated 1:1 ASW. It is sterilized shortly before use by filtration through a sterile Chamberland candle. The salt content of 1:1 ASW was found by experiment to be the optimum for the culturing of *Euplotes taylori*.

From 0.01 to 0.05 cc. of the fluid of each bath is carried over in the transfer of organisms to the next bath. Successful washing requires as long as 8 hours, the *Euplotes* being allowed to swim about in each bath for from 20 to 30 minutes (one to two hours in the middle bath), to rid themselves of bacteria. (We now permit the organisms to remain in the middle bath overnight.) After they are transferred from their last bath to the medium in which they are to be grown, 0.1 cc. samples of this medium and of the last bath are placed upon nutrient agar slants, as tests of sterility. More recently pour plates of the entire last bath have been made. A more detailed study of the washing is now in progress.

In order to determine whether these ciliates, sterile as far as their exteriors are concerned, later defecate bacteria or bacterial spores, which thereby contaminate the medium, the following experiment was tried: *Euplotes*, washed through 9 to 10 baths, were placed in 2 cc. of sterile bran extract in 1:1 ASW and 0.1 cc. portions of this medium transferred to agar slants on each of the 5 following days. This experiment was repeated 5 times. No contaminated slants resulted. The protozoa themselves were not tested for sterility.

Watch glasses in Petri dishes are used not only for washing of the organisms but also for their cultivation. Direct microscopic examination of the culture is thus possible without opening of the vessel. The form of the dish also permits maximum exposure of the organisms to air. From several preliminary experiments in other vessels, particularly in tubes, we are convinced that *Euplotes taylori* grows better in watch glasses than in apparatus where the medium has but a small air surface.

The culture medium, sterilized by filtration, is pipetted in $\frac{3}{4}$ cc. portions into the sterile culture vessel. The washed organisms are added, a sterility test is made, and the dish closed with a strip of surgical adhesive tape. This helps to prevent contamination and minimizes evaporation.

Growth of *Euplotes taylori* on isolated pure strains of bacteria

One of the first media employed by us in preliminary work was an extract of wheat bran in 1:1 ASW. The bran extract was prepared by boiling 1 gram of wheat bran for 5 minutes in 100 cc. of twice distilled water. Five cubic centimeter portions of the extract were then added to 95 cc. portions of 1:1 ASW. Mass cultures of *Euplotes taylori* were obtained for introductory experiments by adding to the medium contained in Syracuse glasses, 100 or so unwashed *Euplotes* and permitting the entrance of atmospheric bacteria by exposure to the air. In a few days a well populated culture was usually obtained.

In order to determine some of the bacterial strains which served for the nutrition of the protozoon, these thriving bran extract cultures were plated out.

Five dominant varieties were isolated. One was recognized as *Sarcina citrea*, a second gave pink colonies and was possibly *Rhodococcus roseus*, while the remaining three which escaped identification are designated here as A, B, C. The classification of the saprophytes is very incomplete and we have had to content ourselves thus far with determining their reactions in the usual standard media.

When washed *Euplotes* were added to the sterile bran extract medium inoculated with one of these five strains of bacteria, it was found that the first two tested in the preceding paragraph were unable to maintain growth of the protozoon. Organisms A, B, C when tried singly were also unsuitable. Not only did C fail to support growth of the ciliate but if added in overwhelming numbers to a culture of the protozoon on A + B, it actually inhibited multiplication of *Euplotes*. For the present we have dispensed with it.

We also used a strain of *Escherichia coli* (*B. coli communis*) described here as K₁₃. This organism has received attention by other investigators studying the nutrition of protozoa and for additional reasons which will be apparent later we desired to use it. By itself, in the bran extract medium, we found that growth of the ciliate was fair or poor. Combined with A and B, themselves poor as food for the ciliate, excellent cultures resulted. It should be added that coincident with the use of *B. coli communis* and the five bacteria previously described, we employed a pure line of *Euplotes taylori* started from a single, sterile, individual.

At this stage of the work we learned through parallel studies that a 0.01 per cent solution of glucose in 1:1 ASW was superior to our bran extract medium in 1:1 ASW. With appropriate bacteria present excellent cultures of protozoa

resulted. In fact the glucose-containing cultures were so densely populated that the use of the bran extract medium was discontinued. This was also regarded as a step forward in the simplification of media. Below are tabulated the results of the experiments with single strains of bacteria or combinations thereof:

BACTERIA	PROTOZOON GROWTH
A.....	None
B.....	None
C.....	None
Coli.....	Fair to poor
A(excess) + B.....	Good
B(excess) + A.....	None
A + coli.....	Excellent
A + coli + B(relatively few).....	Excellent ¹
A(excess) + coli + B.....	Excellent

¹ Many of these cultures were more densely populated than any we have ever seen.

We are of the opinion that B contributes little, if any, to the excellence of a culture containing A + B + coli. Further, many successive subcultures have been made to each of which fresh supplies of A and coli have been added but none of B. These subcultures continued to thrive. Finally if cultures containing these three bacterial strains be plated out it is found that most of the colonies are of A, coli is next in abundance, and B is either a decided minority or may even be so reduced in numbers as to escape detection. The latter grows very slowly.

During the introductory experiments we occasionally observed that the highest division rates followed the use of large numbers of protozoa as inocula. This observation supports Robertson's theory of allelocatalysis (33) referred to in the introduction. On the other hand sterile filtrates of thriving cultures when added to mediocre cultures failed to accelerate reproduction. In addition, such a filtrate

was inoculated with A + B + coli and sterile Euplotes introduced. As a control, a fresh 0.01 per cent glucose medium was treated in the same manner and was inoculated with A + B + coli and with the same number of sterile Euplotes from the same stock culture. The number of protozoa which developed in the latter soon decidedly eclipsed the number present in the inoculated filtrate.

The attempted cultivation of Euplotes taylori on media free of living bacteria

Having demonstrated that the ciliate could be grown in a simple basal medium of 0.01 per cent glucose in 1:1 ASW on simple combinations of bacteria we attempted next to replace the latter by bacterial extracts, simple organic nutrients, and dead bacteria. We first sought an answer to the question of whether the bacteria nourish the protozoa through the secretion of substances of value as food to the ciliate. As an outgrowth of the experiments recorded in the preceding paragraph we added sterile Euplotes to a sterile filtrate of a thriving culture. Since bacteria had been present in great numbers in the parent culture from which the filtrate was derived, it was assumed that the hypothetical nutrient substance should be present. There was no multiplication of the protozoa. We then modified this experiment by the use of a flask as culture vessel into which had been inserted an autoclaved cellophane sac. Sterile 0.01 per cent glucose in 1:1 ASW was pipetted into the sac and into the space which separated it from the flask. The inner fluid was inoculated with suspensions of bacteria A and coli. The next day, the outer fluid, supposedly rich in the products of bacterial growth and secretion, was transferred to the regular watch glasses used as culture vessels. It was found incapable either of sustaining the growth

of added sterile Euplotes or of stimulating multiplication in a mediocre culture.

It occurred to us next that bacteria on disintegration by autolysis might liberate nutrient substances in a form suitable for maintenance of Euplotes. A heavy suspension of A + coli (in 0.01 per cent glucose in 1:1 ASW) was allowed to autolyze over a 10 day period. Even though every organism was not killed, the products of autolysis proved worthless as food for Euplotes.

One reason for selecting the K₁₃ strain of *B. coli communis* for experimentation was that we had at hand through the courtesy of the Department of Bacteriology a very active phage for this strain. The opportunity consequently presented itself of studying lysed organisms as food for protozoa. Preliminary experiments in which coli, as the sole strain of bacteria, gave fair growth of the protozoan, showed that addition of the phage was followed by a failure of growth. The experiment was controlled in the next series by examining the toxicity of Martin's broth alone, and Martin's broth plus phage. The corresponding experimental cultures were in Martin's broth plus phage plus A and coli, and secondly Martin's broth plus A and coli (phage omitted). The results showed clearly that lysis of coli rendered the medium unsuitable for the growth of Euplotes.

MEDIUM	GROWTH OF EUPLOTES
Martin's broth.....	None
Martin's broth + phage + A + coli.....	Poor
Martin's broth + A + coli.....	Good
Martin's broth + phage.....	None—Evidence of toxicity

Many experiments were conducted in which, with bacteria omitted, attempts were made to grow Euplotes on dissolved

foodstuffs. The following substances were tried without securing any multiplication of the protozoa. In every case 1:1 ASW constituted the inorganic medium to which the experimental substance was added in the concentration indicated: .01 per cent sodium lactate, .01 per cent inositol, .01 per cent glucose, .01 per cent ammonium glycerophosphate, .01 per cent alanine, .01 per cent asparagine, inositol plus ammonium glycerophosphate, glucose plus ammonium glycerophosphate, bran extract plus ammonium glycerophosphate. Furthermore, the addition of *B. coli* in most cases failed to so improve the medium as to permit growth of Euplotes. When *B. coli* was added to sodium lactate and to inositol plus bran extract, slight growth of the ciliate was observed. Inositol was tried because of the identification of it by Eastcott (45) as bios I. The use of sodium lactate, glucose, and ammonium glycerophosphate arose from the work of Peters (24) on *Colpidium colpoda*. Five per cent sterile dilutions of rabbit, guinea pig, and horse sera in 1:1 ASW were also found incapable of supporting the growth of sterile Euplotes. The blood sera themselves were presumably non-toxic since the addition of small quantities (0.1 cc.) to 2 cc. portions of cultures of Euplotes on A + coli in .01 per cent glucose failed to retard reproduction. With horse serum only was there any indication of toxicity. This is in agreement with the work of Oehler (31) who failed to grow protozoa on soluble foodstuffs. Finally we attempted to cultivate Euplotes on dead bacteria. *B. coli* suspended in 1:1 ASW was killed by heating at 60°-65° for 1½ hours. To the suspension was added .01 per cent glucose and sterile Euplotes. No multiplication of the protozoon was observed. In similar fashion organism A, killed by heating for 1½ hour periods on

three successive days, failed to support growth. Experiments in which a mixture of the two dead strains was used were unsuccessful.

Ralph Baker, who was associated with us a year ago, attempted the use of toluene-killed bacteria. The toluene was afterwards removed with a current of sterile air. The product failed to support the growth of sterile Euplotes, although as soon as live bacteria were added excellent growth resulted.

Accordingly we have been unable thus far to meet with the success recorded by Tsujitani (7) and Oehler (13, 14) in the use of dead bacteria.

Most recently we have tried, without success, the use of suspensions of disintegrated bacteria, in which the disintegration was effected by exploding with carbon dioxide.

This study, admittedly qualitative, is now being continued on a rigid quantitative basis by numerical counts of both bacteria and Euplotes in the cultures. No mention has been made of pH control. This has been the subject of a separate study the preliminary findings of which demonstrated to us that the extreme limits for growth of Euplotes on mixed bacteria in bran extract were pH 4-9. In our own experiments we have merely endeavored thus far to see that the media employed fell between pH 6 and 8.

Summary

1. The hypotrich, *Euplotes taylori*, has been obtained free of bacteria by repeated washing with sterile artificial sea water.
2. In the presence of suitable bacteria the ciliate grew luxuriantly in a basal medium of 0.01 per cent glucose in diluted artificial sea water.
3. On single strains of bacteria, including *B. coli communis*, and five strains

isolated from a bran extract medium, *Euplotes taylori* grew poorly if at all.

4. On a combination of two of these bacterial strains marked multiplication of *Euplotes* was observed.

5. Sterile filtrates of thriving cultures, bacterial dialysates, autolyzed bacteria, phage-lysed bacteria, toluene-killed bacteria, and heat-killed bacteria failed to support the growth of *Euplotes*.

6. Simple nutrient media, free of bacteria, consisting of various carbon and nitrogen compounds in artificial sea water were likewise unsuccessful.

7. Blood serum in artificial sea water gave negative results.

To the Society of the Sigma Xi we are indebted for a generous grant which assisted in the prosecution of this work. We acknowledge also the courteous coöperation of the Department of Bacteriology in the provision of research space, equipment, and technical aid. Professor C. B. Van Niel was good enough to examine the manuscript and advance several helpful suggestions.

Note added Feb. 11, 1931. We now have evidence that *Euplotes taylori* may be reared, under suitable conditions, on the single organism A. This is now recognized as a large, fluorescent, gram-negative bacillus, giving many of the reactions of *Bacillus fluorescens pseudomonas* (Bergey classification).

LIST OF LITERATURE

- (1) CALKINS, G. N., "Biology of the Protozoa" (Lea and Febiger), 1926, p. 176.
- (2) ———, J. exp. Zool., (1915) 19, 225.
- (3) PRINGSHEIM, E. G., Biol. Centralb., (1915), 35, 375; Arch. f. Protist., (1928), 64, 289.
- (4) PARKER, R. C., J. exp. Zool., (1926), 46, 1.
- (5) LUND, E. J., J. exp. Zool., (1914), 16, 1.
- (6) FROSCHE, P., Centralb. f. Bakt., Orig. (1897), 21, 926.
- (7) TSUJITANI, J., Centralb. f. Bakt., Orig. (1896), 24, 666.
- (8) BEIJERINCK, M. W., Centralb. f. Bakt., Orig. (1896), 19, 257.
- (9) MOUTON, H., Ann. Inst. Past., (1902), 16, 457.
- (10) MUSGRAVE, W. E., and CLEGG, M. T., Dept. of Int., Manila Bureau of Gov. Labs., Bull. 18, (1904); J. Inf. Dis., (1905), 2, 334.
- (11) HARGITT, G. T., and FRAY, W. W., J. exp. Zool., (1917), 22, 421.
- (12) CALKINS, G. N., cited by Hargitt and Fray.
- (13) OEHLER, R., Arch. f. Protist., (1916), 37, 175.
- (14) ———, Arch. f. Protist., (1920), 40, 16.
- (15) ———, Arch. f. Protist., (1920), 41, 34.
- (16) ———, Centralb. f. Bakt., Orig. (1921), 86, 494.
- (17) ———, Arch. f. Protist., (1924), 49, 112.
- (18) PHILLIPS, R. L., J. exp. Zool., (1922), 36, 135.
- (19) CUTLER, D. W., and CRUMP, L. M., Br. J. exp. Zool., (1927), 5, 155.
- (20) CLEVELAND, L. R., and SANDERS, E. P., Science, (1930), 72, 149.
- (21) AMSTER, Centralb. f. Bakt., Orig., (1922), 89, 166.
- (22) HEILBRUN, L. V., Am. J. Physiol., (1923), 64, 481.
- (23) STEARN, A. E., and STEARN, E. W., Univ. of Missouri Studies, (1928), 3, No. 2.
- (24) PETERS, R. A., J. Physiol., (1920), 55, 1.
- (25) PARPART, A. K., Biol. Bull., (1928), 55, 113.
- (26) SEVERTZOFF, L. B., Centralb. f. Bakt., Orig., (1924), 92, 151.
- (27) WALKER, E. L., J. Med. Res., (1908), 17, 379.
- (28) KARTULIS, Virchow's Archiv., (1889), 118, 97. Centralb. f. Bakt., Orig., (1890), 7, 190.
- (29) CASAGRANDE, O., and BARBAGALLO, P., Centralb. f. Bakt., Orig., (1897), 21, 579.
- (30) WÜLKER, G., Centralb. f. Bakt., Ref. (1911), 50, 577.
- (31) OEHLER, R., Centralb. f. Bakt., Orig. (1921), 87, 302.
- (32) CUTLER, D. W., and CRUMP, L. M., Biochem. J., (1923), 18, 174.
- (33) ROBERTSON, T. B., Biochem. J., (1921), 15, 595. J. Physiol., (1922), 56, 404.
- (34) BEERS, C. D., J. exp. Zool., (1928), 51, 121.
- (35) CUTLER, D. W., and CRUMP, L. M., Biochem. J., (1923), 18, 905.
- (36) ———, Biochem. J., (1922), 17, 878.
- (37) GREGORY, L. H., Biol. Bull., (1928), 55, 386.
- (38) YOCOM, H. B., Biol. Bull., (1928), 54, 410.
- (39) MYERS, E. C., J. exp. Zool., (1927), 49, 1.
- (40) GREENLEAF, W. E., J. exp. Zool., (1926), 46, 143.
- (41) WOODRUFF, L. L., J. exp. Zool., (1911), 10, 557.
- (42) GARNJOBT, L., Physiol. Zool., (1928), 1, 561.
- (43) PAGE, I. W., Biol. Bull., (1927), 52, 161.
- (44) HARVEY, H. W., "Biological Chemistry and Physics of Sea Water" (Macmillan).
- (45) EASTCOTT, E. V., J. Phys. Chem., (1928), 32, 1094.



NERVE CONDUCTION IN RELATION TO NERVE STRUCTURE

By R. W. GERARD

The Department of Physiology, The University of Chicago

IT IS historically true in all science that structural knowledge usually precedes functional. In biology, anatomy was far advanced when physiology hardly existed. This is natural enough, since dynamics are more complicated than statics, and since, moreover, the anatomy of a machine may be described with no knowledge of its action while its action is usually meaningless if the structure is not understood. The anatomy may be *described*, but it remains a jumble of parts and dimensions until seen in relation to its function.

In the nervous system, beyond comparison with any other organ, the cell structure and the intercellular connections are so elaborate that even the anatomical facts have been slow to appear. The physiological knowledge is correspondingly very meagre; but enough exists even so to suggest some of the ways in which this complicated structure may be understood in terms of function.

As an indication of the type of correlation possible, it will be recalled that different axons and dendrites in the individual peripheral nerves have variable fibre diameters (96, 127, 128). It is now known that the functioning of a nerve fiber depends in a very direct manner on its diameter and that nerve fibers of larger diameter conduct more rapidly (61), are more easily excited (103, 105), and respond to external influences in different ways than do other fibers of smaller diameter. It has been shown, in fact, that the fiber

groups of a given size tend to carry impulses related to definite functions; the large fibers, for example, carry motor and proprioceptive impulses, the smaller ones transmit impulses aroused by pain stimuli (46, 62).

The above does not imply that for every type of sensation or effector action there exists a unique type of nerve fiber. It has been shown histologically that a single sensory fiber may branch and reach end-organs of quite different anatomical character and presumably, therefore, of not identical function (114, 133). Also, there is physiological evidence in the trigeminal nerve, nearly all fibers of which divide on entering the medulla and run to separate nuclei, that touch sensations are relayed only through one nucleus, pain only through the other (63, 140). The separation of impulses carrying these two sensations apparently occurs at the synapses in these two regions.

The purpose of this paper is to indicate some of the relations that can now be stated or surmised between structure and function in nervous tissue, and still more, to point the direction in which further information is needed. Before considering this problem, it is necessary to introduce some of the present knowledge and concepts regarding the nature of conduction in the nerve fiber and across the synapse.

THE ACTION POTENTIAL

To study nervous activity there must be some means of measuring it or, more

accurately, measuring some change accompanying it. For a millenium the only index of the passage of a nerve impulse in a nerve was the twitch of a muscle innervated by some of the fibers in it. Eighty years ago DuBois Raymond (45) discovered a measurable electric change in the nerve itself. If electrodes are placed at two points on the side of an uninjured nerve and connected through a galvanometer, no current flows, showing that the nerve surface has essentially the same electric potential at all points. If now the nerve is cut or crushed under one of the electrodes, the galvanometer at once gives a deflection, as if the two electrodes were connected to a weak battery and the direction shows that the injured end corresponds to the negative pole. This is the injury or demarcation potential of nerve, the injured part becoming negative to all uninjured points, and remaining so while the nerve is at rest. When the nerve becomes active, the galvanometer shows that the potential difference between the normal and injured points becomes, for a moment, less. Since the injured part does not respond to activity, this must mean that the normal nerve becomes less positive or more negative when active. This is the action potential of nerve, a brief potential change at each region as it becomes active, making it more negative than it is at rest before and after the nerve impulse passes it.

The nerve impulse travels in human nerves at rates up to 120 meters per second (85, 86, 126) (about the highest speed ever achieved in an automobile) and the action potential sweeps along at the same rate (20). This and much more evidence shows that the action potential may be used, with some caution, as a quantitative measure of nerve activity. It is also interesting to note for later reference that the surface of the resting nerve becomes

less positive both on injury and during activity; in the one case permanently, in the other, temporarily. This suggests that activity may involve the reversible breakdown of a structure (membrane).

Only in the last decade have other changes been discovered in nerve during activity. All tissues studied, except nerve, had been shown to increase their chemical activity when functioning. They use more oxygen to burn more food stuff and produce more carbon dioxide and free more energy, mostly heat. The amount of oxygen used can serve as a measure of the increased activity, as can also the extra heat liberated. These measurements have now been successfully made on nerve (44, 52, 64a, 65, 120, 146) and they show that during activity a nerve does use more oxygen and form more heat and carbon dioxide than when at rest, as well as undergo other chemical changes (72, 73, 74, 88, 89); and these new measures of conduction are being utilized along with the action potentials in the study of nervous function.

CHARACTERISTICS OF NERVE ACTIVITY

Using these methods of study, several important generalizations have been reached concerning nerve activity: 1) the nerve possesses an independent irritability (78); 2) a refractory period appears following the conduction of an impulse, during which the nerve cannot be reactivated (6, 27, 33, 76); 3) anatomical and physiological continuity of the nerve fibers is required for successful conduction (56, 78); 4) the nerve impulse can spread in an individual fiber from the point stimulated in both directions (99), even though normal impulses go only in one; 5) the impulses conducted in a single nerve fiber remain isolated in it and do not spread to other adjacent fibers (56, 78, 98, 148); 6) impulses traveling along a nerve may be

reversibly blocked by the action of various agents (144); 7) the impulse carried by a nerve fiber shows an all or nothing behavior (1, 94, 111, 143)—that is, when conditions are such as to permit a nerve impulse to travel, the maximum impulse possible always is propagated; the only alternative is nothing.

1. *Independent irritability.* Normally in the body it is doubtful if nerve trunks are ever directly excited, for impulses are transmitted to them from excited end organs or across synapses. The fibers themselves are, however, highly excitable. A rap on the "funny bone" stimulates the ulnar nerve itself. The sciatic nerve of a frog with attached gastrocnemius muscle is easily dissected out and lives for days with proper care. Such a nerve can be stimulated at the central end and a muscle twitch proves that an impulse has travelled the length of the nerve. A variety of agents may serve to elicit this response: mechanical tapping, application of chemicals, heat, and, best of all, electric currents of all sorts. These latter have been quite widely used to study the irritability of nerves, since they can be accurately measured and delicately graded. It thus appears that when a constant current is led through a nerve by two electrodes, the nerve is stimulated at the negative one, cathode, rather than the positive one (125). It is noteworthy that an active region of the nerve becomes negative, and a region made negative becomes active. Further, the stimulating currents must have a minimal or threshold strength to excite, and this threshold is less for long lasting currents than for short ones (a current lasting one-hundredth of a second is relatively long (100)). Roughly, a certain amount of current must flow to excite and, in a liquid conductor like nerve, this means a certain number of ions must move. This number

we may, for simplicity, consider constant for any nerve fiber in any particular condition.

2. *Refractory Period.* The strength of stimulus required to excite a nerve is greatly increased shortly after a nerve has been active. For one to several thousandths of a second after an impulse has passed down a nerve it cannot be excited at all (the absolutely refractory period (111)), then during the next hundredth of a second (the relatively refractory period), it becomes more and more irritable (will respond to a weaker electrical shock) until it has returned to its normal resting condition. This shows that an important change occurs in the nerve when it is active, from which it rapidly recovers. A similar change occurs in the size of the nerve impulse itself; it is less than normal and travels more slowly than normal when started during the relatively refractory period (111). The change during activity thus affects both "irritability" and "conductivity" of nerve, which then recovers during a refractory period of a fraction of a second. As a matter of fact, the heat production (64) and oxygen consumption (65) associated with activity are not completed for ten minutes or more (at 15°C.) so that a nerve has not fully recovered for this time after becoming active. Action potentials also persist for minutes (9, 67), which, with the chemical changes, may be of importance in determining passage over a synapse.

3. *Antidromic Conduction.* The fact that the nerve impulse travels away from a stimulated point equally well in both directions shows that no pre-existing condition in the nerve determines the direction of propagation, and leads to the conclusion that activity of one place on the nerve is the essential stimulus to neighboring regions.

4. *Isolated Conduction.* Although activity spreads from point to point along one nerve fiber, it does not jump from one fiber to adjacent ones. If this were not true, it would be impossible to detect as separate sensations the touch of two points close together on the skin, nor to contract a muscle slightly while leaving most of its fibers at rest. It will be seen that this limited spread of activity is highly dependent on the nerve structure.

5. *Block.* All the agents that can excite a nerve, and many others, are able to block it when applied more intensely. Cutting or crushing a nerve blocks the impulse at the injured region, but such a block is permanent. A block can be produced at any region along a nerve by heat or cold (28, 35), pressure (116), local anesthetics and narcotics (1, 139, 143, 144), asphyxia (14), electric currents (125), etc., and if done carefully there is no permanent injury. When the agent causing block is removed, conduction past the point of block returns. This shows that conduction requires not only anatomical integrity of the nerve fiber but also an easily disturbed physiological balance. All the agents that cause block, when somewhat less intense, cause depression. A nerve impulse cannot pass at all a stretch of nerve exposed to concentrated ether vapor, but a feeble impulse can pass a stretch exposed to dilute ether vapor. This leads to one of the most important generalizations about nerve conduction.

6. *The All or Nothing Law.* Suppose a nerve passes through a chamber containing dilute ether vapor. It is stimulated at one end and electrodes are placed on the nerve before it enters the chamber, in the chamber, and on the far side, to measure the action potential (and so the intensity of the nerve impulse) at each region. The electrode on the near side

indicates the size of the normal impulse. When the impulse passes on into the ether chamber it is decreased, the second electrode shows a smaller action potential than the first. The interesting question is: What happens to the impulse when it passes out again into normal nerve? It might, of course, remain small as it was in the depressed nerve, but it might also, conceivably, return to normal size now that it is again in normal nerve. This is, in fact, what happens; the far electrode shows the same electric change as the near one (42, 94). The size of the nerve impulse in any particular portion of nerve depends, then, only on the condition of that portion of the nerve and not on the previous history of the impulse. This means, in turn, as has also been experimentally shown (3, 4, 113), that a particular nerve fiber under any given set of conditions can carry only one size of impulse, its maximum for those conditions, or none at all. It responds to a stimulus, either from the outside or from an adjacent region of the nerve fiber, with its all or with nothing.

THE NERVE IMPULSE

From these data emerge certain basic characteristics of the nerve impulse, the wave of change that travels along a fiber and evokes activity of muscle, gland or other nerve cell at its end. The impulse can be started by a stimulus, but once started its propagation continues quite independently. If the initial stimulus sets into action only the local nerve region near the electrode, what starts action in the more distant regions? There seems to be only one answer that fits the facts: The activity of one region of the nerve somehow gives the stimulus to the next region, this to the next, and so along.

The impulse has been defined as "a propagated tendency to excite" (42) and

is often likened to a spark burning along a fuse. In this latter case, heat is the agent that starts a chemical change at some point; the reaction liberates enough heat to start the same change in the next region, the heat from this starts a third point, etc. If the initial heat applied (stimulus) will just start the reaction, its further travel goes on automatically. The size of the spark depends only on the fuse in which it travels. If it reaches a damp region, it becomes feebler, or goes out and is blocked; but if not blocked, when it passes on into dry fuse, it flares up to its normal size. In the nerve, also, the stimulus starts a chemical change, and this starts the same change further along, but the means by which the first change brings about the second is not so simple. It does not seem possible that it does so by means of a rise in temperature, for a single impulse raises the temperature of the nerve hardly one ten-millionth of a degree (64). It has been noted, however, that electric currents, or ion changes, easily excite nerve on the one hand, and, on the other, move along it with the impulse. It seems very probable that these currents in the nerve are the means of excitation of a resting region by an active one; and since ion movement is determined by resistances, polarization and the like, which are in turn expressions of structural conditions, it is not surprising to find that the further analysis of conduction in the nerve fiber enters at once into questions of its morphology.

The general view of the nerve impulse now held (41,106) is somewhat as follows. Consider a nerve fiber as consisting of a cylindrical mass of protoplasm surrounded by a (plasma) membrane and lying in tissue fluid. The protoplasmic core contains salts and other ions that can freely move about in it, and the tissue fluid is similar in this respect. The membrane

separating them, however, contains few ions and offers great resistance to the passage of ions through it. It has, therefore, a high electrical resistance, and this has been actually determined (127). The material of which the membrane is composed, at least in part, is assumed to be chemically very active so that it breaks down under certain conditions in an explosive fashion. It is also probable that this membrane is polarized at rest with more positive ions on its outer surface and more negative ions on its inner one. When the membrane is broken down, ions are able to pass through and neutralize the inside and outside (see Fig. 1). This explains why an injured part becomes less positive than an uninjured one and why a similar change toward the negative ap-

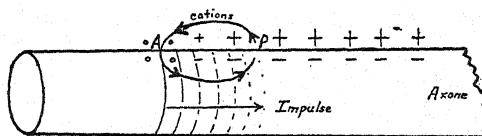


FIG. 1. MODEL OF THE NERVE IMPULSE

For explanation see text

pears at an active region, for the electrodes record the condition at the outer surface of the fiber.

When an electric current is led through a nerve, the electrodes are not on the individual axons but are in contact, through the perineureum, with the tissue lymph or fluid. Positive ions migrate away from the positive pole along the nerve toward the negative pole, and negative ones in the reverse direction. Most of them will move freely in the tissue lymph, but some must come against the nerve fiber membranes. Near the anode, positive ions will move from the fluid against the membrane; near the cathode negative ones will do the same. In the fiber cores ions will also move, positive ones towards the cathode, negative toward

the anode, until they reach the membrane. Near the cathode, then, negative ions move to the outer surface of the membrane from the surrounding fluid and positive ions move to the inner surface from the axon core. The reverse occurs at the anode. The resting membrane, we have decided, is polarized with extra positive charges on the outside and negative within. The applied current, then, will increase the polarization near the anode, but near the cathode new ions which move to the membrane neutralize those already there. At the cathode the membrane is depolarized, and it is here that the nerve impulse starts when stimulated by the applied current.

The next step is largely hypothetical. It is assumed that the depolarization of the membrane somehow affords the condition necessary to set off the explosive chemical change in the membrane itself. As soon as this happens, or possibly as a direct result of depolarization, the resistance to ion movement through the membrane disappears at this point, very much as if the insulation of a wire were scratched off there. Now, quite aside from any current sent into the nerve from the outside, further changes must follow. The membrane next to this active region is still in its resting state, polarized with positive ions outside and negative inside, but they are no longer held apart by an intact resistant membrane. Ion streams are able to pass through the active broken down region close by, and rapidly do so. This, in turn, depolarizes the region of the nerve next to the first one and, of course, the chemical change occurs here and the membrane becomes permeable. In this way, it is obvious, a wave of electric and chemical change must spread along the nerve fiber in both directions from the point first stimulated. This is the nerve impulse, a propagated excitation.

Certain steps in this development are hypothetical, and it must be recognized that the picture has been simplified to a merest skeleton. The action potential, for example, may not represent a passive depolarization but a potential actively produced by the chemical reactions. But whatever the details, it is highly probable that the nerve impulse consists basically of a local membrane change of a chemical and physical nature, which leads to flow of ions, or current, which in turn starts the local membrane change at adjacent points. This accords with all the facts detailed above, and Lillie (106) has happily developed a model which is known to depend on such a mechanism and which transmits "impulses" that conform to practically all the properties of the nerve impulse.

This consists of an iron wire surrounded by a membrane of iron oxide and lying in nitric acid. When current is passed into it, a wave of break-down of this surface film starts at the cathode and travels along the wire accompanied by an action potential. After the membrane is rapidly broken down, in the wire as in the nerve, it reforms more slowly, leading to a refractory period during which a second impulse is transmitted feebly or not at all.

PART II

The structural complications of the situation can now be considered more exactly. A myelinated nerve fiber is not a tube of homogeneous protoplasm with a membrane around it, as has been abundantly demonstrated by histological studies (114). The axis cylinder contains fibrils and axioplasm limited by a membrane, the axiolemma. A questionable periaxial space separates this central cylinder from an investing layer of myelin, surrounded in turn by a sheet of thin nucleated cells of Schwann. The whole

is still further enveloped in fine divisions of the connective tissue framework of the nerve trunk which pass in from the perineureum and form capsules about individual nerve fibers (sheath of Henle) and groups of them. Longitudinally also there is no homogeneity. At intervals of half to several millimeters, at a node of Ranvier, the myelin is discontinuous, the neurilemma or Schwann sheath dips in towards the axon core, and the core itself is markedly constricted by a "thorny collar." The myelin is further broken between the nodes by oblique conical slits (of Schmitt-Lantermann) in which lie coiled fibrillar structures (Golgi-Reznikoff apparatus) and, even where seemingly homogeneous, a laminated and reticular structure has been ascribed to the myelin substance.

How is the flow of ions, on which propagation depends, influenced by the neurofibrils, the periaxial space, the fatty non-conducting myelin with its slits of Lantermann and interruptions at the nodes of Ranvier, the neurilemma, sheath of Henle, etc.? What is the hypothetical membrane—the surface of each fibril, the axiolemma, myelin, Schwann sheath? Most of these questions, of course, cannot be answered, but it will be interesting to examine the evidence on a few specific points.

Though probably of little significance for the normal activity of nerve *in vivo*, the perineurium has been very important in obscuring the properties of the axones in *in vitro* studies. This dense sheath resists the passage through it of ions or molecules. Thus it tends to distort action currents passing from the axones to the recording instrument (26), and to mask the action of potentials applied to stimulate. Recent work (24) makes it probable, for example, that the ordinary failure of a constant current to cause repeated

responses of nerve during its passage, which it should do according to the theory outlined, is due to the inert sheath around the nerve. The diffusion of substances between an outside solution and the interaxonal fluid is greatly retarded. Narcotics act on nerve most rapidly where branches perforate the sheath (130). Methylene blue hardly penetrates the whole nerve but stains it rapidly when the sheath is longitudinally slit (51). The same procedure causes a nerve to block in isotonic glucose or potassium chloride solution in a few minutes rather than several hours, owing to more rapid diffusion (51).

NEUROFIBRILS AND FIBRE TYPES

Assuming the normal existence of neurofibrils, at least in invertebrate nerve (30, 41), what evidence bears on the view that they rather than the axis cylinder as a whole represent the conducting units? Histologically, they are seen to cross the region of the nodes unmodified (118) and, possibly, even to cross the synapse (84), whereas the axis cylinder is markedly constricted with reduction of axioplasm at the nodes and similarly where it leaves the cell body (118). The fibrils, it has been claimed, become finer and more numerous as a nerve is fatigued (114), suggesting a functional change; and Peterfi (124) has recently seen fibrils appear in vertebrate nerve while it is active. On the other hand, astrocytes, without evident conducting function, may have marked fibrils (15).

Conduction is supposed to require oxidation of some substance in a membrane. From the heat produced during conduction the number of molecules of food substance oxidized can approximately be calculated. When the area occupied by such molecules is obtained and compared with the area of the axiolemma, it appears that they would

occupy only a minute fraction of it, a twenty-thousandth (44, 71). (Of course exothermic reactions might be partly balanced by endothermic ones.) If only the surface of a few neurofibrils becomes active, a more probable ratio would be obtained.

Still another observation might be explained in terms of neurofibrils. It has been shown in the dog that the nerve impulse traveling up a sensory nerve is delayed 0.00014 second in passing the spinal ganglion (47). Each nerve fiber is connected by a single T branch with its monopolar cell, and it might be assumed that the impulse has to travel along this branch to the cell body and back before proceeding into the cord. At the usual rate of travel this delay would correspond to a detour of 6 mm. each way. The main difficulty in the case of an impulse involving the whole axis cylinder is the refractory period. The branch could carry the impulse to the perikaryon but would then be refractory to its return for very much longer than .0001 second. If, however, neurofibrils carried the impulse there would be no necessary conflict; for each fibril ascending the nerve might turn into the branch, run into the cell, possibly around the nucleus, continue back into the branch and so on up the dorsal root. The impulse would then not have to retrace its path along the fibril and the refractory period would not come into question.

There is, unfortunately, a new difficulty with this explanation, aside from the absence of certain histological evidence as to whether or not the fibrils, like the axon, form a T with only one branch to the cell. If the nerve impulse must indeed follow a path leading into the nerve cell, removal of the cell body should block conduction even though the fiber beyond the T branch remains intact. The experiment was performed last century (21). In a crustacean the ganglion on the nerve supplying an

antenna is sufficiently pedunculated to permit its excision, and conduction was reported to remain intact. Also, Steinach (139) observed conduction through spinal ganglia of vertebrates after the cell bodies showed marked histological degeneration due to obstruction of the blood supply.

This leads us to consider some of the evidence against the neurofibrils being the conducting units. The all or nothing behavior of nerve might be equally valid for the entire axon or the individual fibril. For any nerve, however, the number of the all or nothing units would be far greater in the case of the fibrils than the axon. For a very fine nerve, with only a dozen axons, the number of units has been measured by the muscle response (2, 8). Thus a very weak stimulus should excite only the most sensitive unit and give a certain sized twitch, a slightly stronger stimulus would excite the two most sensitive units and give twice the twitch, and so on until all units are stimulated and the maximal twitch observed. Actually the number of units found agrees with the number of entire axons and is far less than the number of fibrils. A similar analysis by action potentials has been made for muscle fibers (2). It might be argued that conduction is none the less in the individual fibrils and that all those in one axon are, even though reaching different muscle fibers, always active together. But another important group of observations cannot be easily reconciled with this suggestion.

The threshold of any one axon in a nerve trunk, the rate at which it conducts an impulse, and other properties have been shown, as mentioned earlier, to depend on the diameter of the fiber. A fiber with a diameter of 18μ transmits an impulse twice as rapidly as one of 9μ and three times as rapidly as one of 6μ . (This relationship does not hold for still smaller fibers (49)). This has been established by studying the

shape of the action potential in different nerves and at different distances from the point stimulated. As the distance over which the impulse has travelled is increased, the action potential in those fibers transmitting at a rapid rate will be a little ahead of that in the slower ones, and by careful study the actual rate of conduction in different fiber groups can be accurately determined. These are known to differ from one type of nerve to another, and histological examination of these nerves permits counts and measurements of the individual axons to be made. A comparison of the two sets of data gave the results stated (Gasser and Erlanger (46, 62)).

It thus appears that nerve conduction is, over a considerable range, a simple function of axon diameter. This would rule out the fibrils if the large axis cylinder differs from the small simply in the number of fibrils it contains. If it could be shown, however, that the individual fibrils vary in size as does the entire cylinder, the possibility of their acting as conductors would remain. There is another way, also, in which these facts might be interpreted in terms of fibrillar conduction. An examination of the way in which diameter affects conduction rate is first necessary. Before pursuing this subject it will be interesting to see other ways in which this morphological-physiological correlation is likely to be extremely valuable.

The ventral roots of spinal nerves consist almost entirely of large fibers; the dorsal roots mostly of smaller ones of varying size (46, 96). This would suggest that the large fibers with more rapid conduction and with lower thresholds are essentially motor in nature, leading to contraction of muscles, which accounts for the experimental fact that when mixed nerves are stimulated in humans, muscle twitches can be obtained at intensities of excitation too low to cause sensation.

The dorsal root contains a few large fibers, many medium sized and many fine fibers (46, 96). The largest fibers are distributed through muscular branches of the nerve and are proprioceptive in function. The medium sized ones carry impulses leading to sensations of touch and temperature, the latter nerve fibers being somewhat smaller, and the smallest carry impulses which reach consciousness as pain. These facts have been established by the use of different types of nerve block (62). Thus, for example, it is known from clinical experience and animal experimentation that cocaine abolishes conduction in peripheral nerve in the order: pain, temperature, touch (147), whereas pressure abolishes the ability to receive these sensations in the reverse order (87). Applying these methods of block to isolated nerves and studying the action potentials, it is found that the slowest impulses, representing the smallest fibres, disappear first under the action of cocaine and last under the influence of pressure.

A similar analysis of fiber groups in terms of function is being pursued into the white and gray rami communicantes of the sympathetic system and into the various sympathetic nerve trunks in the body, as the splanchnic and vagus (parasympathetic) (49, 82). In this latter, at least seven types of fibers are present and it is only a matter of further experimentation to assign to each type one or more of the many activities mediated through the vagus. It has just been reported, for example, that all heavily medullated fibres are somatic, afferent and efferent, the relatively thinly medullated ones are visceral afferent, and the very thinly medullated and non-medullated ones are visceral efferent (81). Obviously, a great field is opened up in the analysis of the functional components of nerves in terms of their fiber population, and with this added clue, nerve connections and patterns in the central nervous

system may be considerably further elucidated.

Returning to our schematic picture of a cylindrical core, surrounding membrane and outside fluid, what determines the rate of propagation? Consider a point (P) on the resting membrane a short distance from an active point (A) (Fig. 1). P becomes active when a certain change in ion concentration has developed there. Ions migrate to or from P under the influence of a potential difference between active and resting points. But the number of ions moving across any section determines the current flowing and, for any given potential, this current varies inversely as the resistance of the path it must follow. The path of positive ions, as has been developed, is from P through the outside fluid to A and from A through the inner core to P . Finally, it will be recalled that the resistance of any conductor increases as its length increases and decreases as its cross section increases. We now have an explanation at hand for the relation of axon diameter and conduction rate. The speed of conduction will be greater or less as it requires a shorter or longer time for P to become active after A is active, or conversely as a point, P , further from or nearer to A becomes active in a given time. This in turn depends on the time necessary for a definite number of ions, or a given amount of current, to flow between A and P ; and, since the number of ions flowing varies inversely as the resistance, this becomes a determining factor. When the sum of the outer resistance between P and A and the inner one between A and P becomes twice as great, ions will move at half the speed, the needed number will accumulate in twice the time and the rate of conduction will be halved.

In the case of the large fiber versus the small, considering the axiolemma as the membrane involved, the outside resistance

through the abundant tissue fluid may be assumed to be low (see later, however), while that of the core is large. The greater the diameter, the lower the core resistance, then, and the faster the conduction. It might seem at first that, since the cross-section and resistance vary as the square of the diameter, the rate of conduction should also do so. But the membrane area increases with the core diameter and, in a manner of speaking, each portion of the membrane shares the conducting core with all the other portions, so the greater membrane area (varying as the first power of the radius) partly offsets the increased conductivity (varying as the square of the radius).

What would be the situation if the fibrils were the conducting units? Then their cores (assuming that they have a fluid core surrounded by a membrane, which is very doubtful if they are of micellar nature (123)) would be the inside resistance and the axioplasm the external resistance. If the inside resistance were the main one, then variation in fibril diameter would act as variation in axon diameter in the case just considered; and if fibril diameter and axon diameter varied together, it would be impossible to decide which was the conducting unit. On the other hand, if the fibrils had a low core resistance compared to that of the axioplasm (which is not likely since their cross section is so much smaller), a new possibility arises. The conduction rate would then depend on the axioplasm, now the external resistance, available for each fibril. One axon of twice the diameter of another, and therefore four times the area, would conduct at the same rate as the second if it also had four times as many neurofibrils, since the axioplasm for each would not be changed, but four times as fast if it had the same number of fibrils and four times as much axioplasm (one-

fourth the outside resistance) for each. Obviously, we are back to a cytological question: how does the number and size of the neurofibrils vary with the diameter of the axis cylinder?

Another point may be mentioned before leaving the fibril question. The nerve in the foot of a large slug is very extensible. The time required for an impulse to pass along the nerve when shortened was found (36, 92) to be less than when the nerve was stretched. This precludes conduction in a solid structure that might be coiled or extended, since the distance the impulse must travel would then be the same for any position. Of course, the neurofibrils are not now regarded as such inextensible solids.

As will be seen from the evidence considered above, it seems unlikely that the neurofibrils represent the true conducting units of the nerve cell; and certainly non-fibrillar cells, as the fertilized sea-urchin egg, show membrane transmission. It must be kept in mind, however, in considering the relation of diameter to fiber activity that no fiber has a uniform diameter. The axis cylinder is much constricted at each node and near the cell body and is usually quite irregular near an end organ or synapse, and it is claimed (22) that local compression of a nerve does not block conduction when the perifibrillar substance had been squeezed to 1/600th its normal cross-section providing the fibrils retain their normal staining properties. The fibrils presumably are more uniform throughout. Some further considerations of the diameter-conduction relation will be mentioned later. Physiologists have quite regularly assumed that the axis cylinder as a whole is the fundamental unit of conduction. Histologists have been more divided, some, impressed by the anatomical availability of the fibrils, having leaned more to the view that conduction occurs

along them. Bethe (22), for example, attributed conduction entirely to the fibrils, the remainder of the cell serving a "trophic" function. The recent, exactly opposite, suggestion of Parker (121), that the fibrils carry nutritive influences is at present purely speculative, and an older idea of their serving as a supporting skeleton is hardly tenable (75). A final answer is, obviously, not yet at hand, and equally obviously, cannot be obtained by either the morphologic or functional approach alone, but only by a proper utilization of both together.

THE RÔLE OF MYELIN

The relation of myelin to nerve function has been a matter of even greater uncertainty than that of the fibrils, and the significance of the nodes of Ranvier has been particularly elusive. Myelin is composed of fat-like material which is very little ionized and a correspondingly poor electric conductor. The suggestion at once comes to mind that the highly resistant membrane needed for propagation of the nerve impulse is the myelin sheath. This cannot be the general case, however, for non-medullated nerves conduct perfectly well. Indeed, it is now fairly certain that fibers normally myelinated can conduct while lacking their myelin, as is the case in late embryonic development (10) or during regeneration. Thus, the longitudinal tracts in the rat's spinal cord are not yet myelinated at birth, but stimulation of the tail evokes responses by the head (70).

Another obvious suggestion is that the myelin acts as an insulator to the axis cylinder and prevents action currents from one fiber from stimulating adjacent ones. That some effective insulation does exist is shown by the fact of isolated conduction previously discussed. But isolation of impulses is also the case in unmyelinated

nerve bundles, though probably not so perfect in these. It may be of significance in this connection that as fibers approach their peripheral endings where, instead of conduction, reaction with other tissues is important, the myelin is invariably lost; and the same is true where fibers meet other nerve fibers or nerve cells, as in the grey cortex or other regions of neuropil (1114).

The rôle of the myelin should be most directly suggested by a comparison of the behavior of medullated and non-medullated nerves. One striking difference is in conduction rate, which is much greater in medullated nerves. The non-myelinated fibers are smaller in diameter than the axis cylinder of most myelinated fibers, but the difference in speed of conduction is more than would be expected on this basis (49). How might myelin affect the rate of passage of the nerve impulse?

It was assumed in the discussion of the influence of fiber diameter on conduction rate that the resistance outside of the membrane (we will assume this to be the axiolemma) was low because of the large amount of tissue lymph present. If this resistance were increased conduction must become slower. But plastering an axis cylinder with a good layer of resistant myelin must certainly insulate it to a marked degree from the tissue fluid. The outside current between the resting and active points of the membrane must then flow in the minute periaxial space or through the openings in the myelin to and from the tissue spaces. In either case it might be expected that conduction would be greatly slowed in the medullated fibers, whereas the reverse is the case. Another structural fact enters, however, in the existence of the nodes (and incisions of Lantermann) and this greatly changes the conditions of current flow.

In the bare membrane considered before, when point *A* is active current flows be-

tween it and point *P*, as discussed; but it also flows to a greater or lesser extent to a great many other points nearer to or farther from *A*. It was merely convenient to consider a single point *P* in the discussion; actually a large area of the resting membrane is involved in the ion movements, which are consequently rather diffuse. With myelin insulating most of the membrane but with naked axis cylinder exposed at the nodes, the ion flow would be more nearly as in the diagrammatic case and the action would be concentrated at the exposed points. It is conceivable that this would result in the excitation of a more distant resting point by an active one, and that the nerve impulse would, in a sense, jump from node to node. Lillie (110) has, in fact, demonstrated something of this nature with the iron wire model. The wire lying free in nitric acid conducts rapidly. When it is surrounded by a glass tube it conducts more slowly, and the smaller the tube diameter, the slower the conduction. This agrees well with the influence of axon diameter in the nerve itself. If, now, a narrow glass tube running the length of the wire and causing very slow conduction is broken across at several points, thus simulating the nodes in the myelin sheath, the conduction becomes more rapid than when no tube is present and the activation can be seen to jump from node to node.

If such a mechanism does operate in medullated nerves, it is obviously of great importance to know in much greater detail than at present the distribution of the nodes of Ranvier. It is highly interesting that a direct relation does exist between internode length and axon diameter (in large frogs, for example, 7μ fibers have an average internode length of 1050μ ; 14μ fibers, of 2000μ (29, 79, 145)), and it is not impossible that the apparent relation between diameter and conduction rate is

really one between rate and internode length. This length increases faster than diameter as the frog grows larger (79), and, for a given sciatic nerve, may be as much as 30 per cent greater in the lower portion than in the upper (79). Careful measurements of conduction velocities being made on comparable material should help decide between the two possible mechanisms. Certainly, as the thickness of the myelin sheath becomes less from one fiber type to another, conduction rate decreases more than could be accounted for by any diameter change. If the stimulating action currents are in fact effective from node to node, the constriction of the axis cylinder with reduction of axioplasm at just these points would render the neurofibrils especially open to activation by them. The thorny collar and transverse plate described at the nodes (118) and in relation to the fibrils would acquire an important functional significance.

It may also be noted in passing that different nerves regenerate after injury at different rates (0.5-2 or more mm. per day). Since the neurilemma appears to enter into regeneration (though not indispensable for it) and there is one Schwann nucleus per node, node counts on various nerves might provide an understanding of these differences.

In the central nervous system, myelinated nerve fibers have no nodes of Ranvier (129) or, according to others (23), nodes at very short intervals. In either case they should conduct at relatively slow rates. The division of axons and dendrites into fine terminal branches should act in the same direction. In all reflex responses, when the time between stimulus and action is determined, there appears a considerable interval beyond that needed for conduction through peripheral nerves to and from the spinal cord and for the effector organ to begin its activity (54, 93). (Beritoff (19)

has recently questioned this). This interval is assumed to be the time required for the nerve impulse to pass over one or more synapses. It is not impossible, however, that a large portion of it is due to slow conduction along intraspinal nerve fibers.

During ether or chloroform narcosis of a nerve the myelin swells and irregularly decreases the diameter of the axis cylinder (104). This may explain, in some part, the slowed conduction and depressed responses obtained from a partially anesthetized nerve. Similarly, polarization by a constant current causes, by electro-endosmosis, decreased fiber diameter at the anode and increase at the cathode (13, 135), and conduction rate is altered in the same sense (25).

Another difference between nerves with and without myelin is related to their metabolism. It is generally true that non-medullated nerves fatigue more easily than medullated ones (59, 107). The idea that myelin may serve as a food reserve for the active axis cylinder is an old one, but far from demonstrated. It is now known that nerves do not burn sugar for the extra energy used in activity (89), and changes in phosphorus combination in the nerves suggests that they may burn phospholipins (74). A change in myelin structure accompanying brief activity of a nerve has been reported (13, 95, 142). Also, the appearance of the myelin, as studied under polarized light, alters when a current is passed through a nerve; and a lecithin emulsion can be made to show similar effects (138). When studied in the dark field changes in salt content of the bathing fluid cause rapid alteration of the appearance of the myelin. Salts and polarizing currents may have an interdependent effect on nerve conduction as well as on its staining properties; though the latter is affected only by much more severe treatment (95, 135). Finally, it is well known that

myelin shows marked histological and chemical changes during ordinary degeneration and regeneration of nerve (90, 117). But these problems lead too far into nerve metabolism to be followed here.

It appears, then, that the presence of myelin, and particularly its segmentation, must lead to changes in the electric circuits through and around nerve fibers. If conduction of the nerve impulse depends, as is believed, on the flow of currents, the myelin sheath must exert a profound influence upon conduction, though possibly not in the manner suggested above. Besides a physical effect, there is the further possibility that the lipins of the myelin may play a rôle in the chemical sequence of nerve activity; and this problem is being further investigated.

PART III

PROPERTIES OF THE REFLEX ARC

We have so far considered only the conduction of the nerve impulse along an essentially uniform, unbranched nerve fiber. This is the simplest case, and, therefore, the most studied, but it is obvious that the properties of peripheral nerves are not identical with those of the whole nervous system, or even of the simple reflex arc.

The reflex arc shows many new properties or at least very great quantitative changes in those of the nerve (58, 130). For example:

1. *Fatigue.* Although the nerve fiber is fatigued with difficulty and in myelinated fibers at least never to inactivity (30, 68), fatigue of reflexes is rapid and marked in many cases (69).

2. *Drug Action.* The nerve fiber can be blocked by the various narcotic drugs when they are present in sufficient concentration; the amount necessary to produce an effect on the peripheral nerve, however, is often hundreds of times as much as

that needed to abolish reflexes. Strychnin, morphin, caffein, and the like, all will act on the nerve fiber in sufficiently great doses, but as ordinarily used in pharmacological or therapeutic work, their action on the central nervous system is manifested in amounts incomparably less.

3. *Irreversibility.* Whereas the nerve fiber conducts equally in both directions, conduction in the reflex arc is unidirectional; activity passes freely from the sensory nerve into the central nervous system and out by the motor, but stimulation of the central end of the motor nerve leads to no activity of the sensory one (18, 112).

4. *Variability.* The single nerve fiber responds in the most invariable manner possible, all or none. Although the *all* is dependent on the condition of the fiber and, therefore, can be modified by various agents, the amount of variation is negligible under conditions even approximating those in the body; the nerve impulse is therefore practically constant in any fiber. Not so the reflex response. The latent period between stimulus and response, the intensity of response to a given stimulus, even the appearance or non-appearance or the type of response, are all subject to great variation with differing conditions of the central nervous system.

5. *Latent Period and After Discharge.* The nerve fiber begins activity within five hundred thousandths of a second after a stimulus is given (48), and stops as soon as stimulation is over. A reflex response may appear some seconds after the stimulus has been given and, conversely, after stimulation stops the response may continue for some time.

6. *Summation.* If one or a few closely spaced stimuli to a nerve fiber do not excite it, further repetition of the same stimulus will not do so. A reflex response will sometimes follow hundreds of repetitions

of a stimulus which in any shorter sequence would remain ineffective. There is a marked summation of stimuli.

7. *Inhibition.* The converse of this is also commonly seen in the reflex, but only under very special conditions in the nerve fiber. Impulses reaching the central nervous system by certain nerves are able to inhibit reflex responses produced by other nerves at the same time.

8. *Independent Rhythm.* The nerve fiber ordinarily responds to each stimulus given with one response as long as the stimuli are spaced sufficiently far apart so as not to encroach on its absolutely refractory period. It is thus able to respond with 500 or more impulses a second. In the reflex, the rhythm of response is rarely closely related to the rhythm of the stimulus, although in certain types the response may follow frequencies up to 100 a second or more (39, 40, 58, 108).

Since these new properties appear in the central nervous system, it has been natural to look for their explanation in some structure or mechanism not present in the peripheral nerve. The region of junction between two nerve fibers is obviously a new feature and must involve some differences in behavior, so that these properties are usually credited to the synapse itself. The discussion to follow will assume that this is the case, though, in fact, it is not at all certain that many of them are not due rather to interposition of cell bodies and dendrites. For example, greater fatigability and susceptibility to drugs would be expected in a region with a higher metabolic activity. The gray matter of the central nervous system has a metabolism at least seventy times as intense as that of the nerve fibers (66, 115, 134), so that if the latter would require three hours to asphyxiate, the nerve centers should require only about three minutes. A recent observation that antidromic impulses along

motor fibres cause histological changes in their cell bodies while not acting on the synapsing neurone suggests, however, that the point of block is at least on the dendrite side of the cell body (80).

There have been described many types of synaptic connections between axons and dendrites (114). An axon and dendrite may meet simply tip to tip, or may run parallel and in contact for a considerable distance. An axon may twine about a dendrite, end as a knob or plate on a dendrite or cell body, or one or more axones may form a complicated network with dendrites, even to the extent of producing a well defined glomerulus surrounded by a connective tissue capsule. Fibrils may pass across the boundaries of the processes, at least in certain preparations, or not, and all degrees of intimacy of connections have been seen. There are also many physiological types of reflex arcs. The existence of any correlation between functional and anatomical types of reflex connections has not yet been demonstrated, though it may be assumed to exist.

The different kinds of reflexes may be demonstrated in a dog with its spinal cord cut in the thoracic region (136). Among the many reflexes of the legs of such an animal are: the flexion reflex, a pulling away of the leg from a painful stimulus on the foot; and the crossed extension reflex, a stretching out of the opposite leg at the same time. These two reflexes behave very differently in regard to latent period, summation, after discharge, and many other points (58). The flexion reflex appears fully formed in response to a single stimulus; the muscle contraction rate will follow the rate of stimulation up to one or two hundred a second and as soon as the sensory stimulus is stopped, the leg relaxes. The crossed extension reflex does not appear so easily in response to stimulation and can almost never be elicited with

any force by a single excitation. It grows progressively, owing to summation as the afferent impulses are repeated, persists long after they are stopped, and is easily inhibited by still other afferent activity. In the flexion reflex, when the leg flexors contract, the extensors of the same leg simultaneously relax. In the crossed extension reflex, similarly, while the extensors are contracted, the flexors are relaxed. Instead of stimulating the skin of a leg to produce these effects, the afferent nerve from that skin region may be used. Thus, stimulation of the popliteal nerve on the right side will lead to contraction of the flexor muscles on the right side and the extensor muscles on the left side, and relaxation of extensors on the right side and flexors on the left, while stimulation of the left popliteal does exactly the reverse.

It will thus be seen that somewhere in the connections of the afferent neurons with the efferent, there are mechanisms permitting a single afferent fiber to produce motor discharges of a certain type on one side of the cord, of a different type on the opposite side and inhibition of the activity of other motor neurons on both sides.

PHYSIOLOGICAL MECHANISMS OF THE SYNAPSE

The attempt was made for many years to account for these additional properties of the reflex arc by a sufficiently intricate set of connections, having only the known properties of the nerve impulse in the peripheral fiber (111). In recent years this attempt has been largely forsaken as futile and new physiological mechanisms are now assumed to come into play across the synapse. There appear to be two main ways in which a nerve impulse travelling along an axon can initiate activity of an adjacent dendrite and start a similar nerve impulse in it. Either the same kind of ion migration and chemical response which

represents successive activation of one region of the nerve fibre by another must also take place at the synapse, or it is conceivable that the end of the axon acts as a miniature gland and, when stimulated, produces some chemical which is able to excite an adjacent or neighboring dendrite.

An interpretation of central inhibition, summation, and other properties has been offered mainly in terms of the second concept by Sherrington (137). Thus, if one impulse travelling over one axon produces a given amount of exciting substance, two impulses over one axon, or one over two, should give twice the amount. If all this substance becomes effective on a dendrite of a second cell, then stimulation of more afferent fibers or more frequent stimulation of the same afferent fibers should have greater effect. This is exactly what happens, the latent period being decreased and the number of responding motor cells increased under either of these two conditions. Also, if a large amount of excitatory substance has accumulated by repeated or intense stimulation, it will take some time for it to disappear, and during this time the motor discharge should continue. If certain types of axon endings produce excitatory substances or changes, other types of endings might equally well produce inhibitory substances which tend to neutralize the excitatory, the two summing algebraically. The correct prediction may be made that if the right and left perineal nerves are stimulated at the same time, since one tends to excite the flexors of the right leg and the other to inhibit them, the result actually obtained may be nil. (More commonly, alternate stepping results—which is less simply interpreted.) It is certainly of importance in this connection that there are morphologically different synapses made by various axons in connection with a single cell (16), so that the possibility of different end-effects by

these axons is at least histologically justified.

For this view it is not particularly important whether a membrane, separating the two cells at the synapse, is present or not; although the former condition is more or less implicitly assumed. Even for the more physical interpretations of conduction across a synapse, the presence or absence of a membrane similar to that around the fiber is not of vital importance. It will be readily seen, in terms of the previous discussion, that a transmitted membrane change, which constitutes the nerve impulse, might quite easily involve a membrane separating two cell processes, so that it would actually help in the transmission of the impulse across the boundary.

The physical interpretations of synaptic conduction depend in more detail on the known properties of conduction in nerve fibers. Thus, it will be recalled that a fiber of large diameter has a lower threshold and reacts more rapidly than a smaller fiber. It is quite conceivable, then, that if processes of small and large diameter were in contact, or even in continuity, that an impulse travelling along the small fiber might successfully pass on into the large, which has a lower threshold, whereas the reverse might not be true. The junction of a fine and coarse fiber, then, would account very simply for irreversible conduction in the synapse (53). Further, any two fibers of different thresholds—that is, requiring electrical currents of different intensities and durations to activate them—might not be able to stimulate one another. If these characteristics of excitability were modified, new patterns of response would result. Bremer (34) has found that the afferent fibers of a spinal nerve have a threshold quite similar to the efferent fibers going to flexor muscles, whereas the fibers to extensor muscles have a quite different threshold. Under the action of strychnin,

all thresholds are lowered and become similar. The result is that the afferent impulses normally producing contraction of the flexors only now lead to contraction of flexors and extensors together, and a general muscular spasm results. A similar relationship between threshold of nerve and of the muscle to which it goes has been elaborated by Lapicque (101, 102), who explains the action of certain paralyzing drugs, such as curare, in terms of their ability to change the threshold of one tissue and not the other. (This has been seriously questioned by Rushton, 132.)

As further evidence on the question of irreciprocal conduction in the synapse, some recent work (12) has shown that such conduction may be established in tissues where there is unquestionably protoplasmic continuity. If a sartorius muscle, with parallel fibers running nearly its whole length, is stimulated at either end the excitation is transmitted the whole length of the fiber and it all contracts. If the muscle is compressed by a horizontal surface in the center, conduction from either end is blocked at the same time. If, however, it is compressed at the center by a tilted surface, so that the pressure at one side is established sharply and at the other side gradually, it is found that conduction is blocked in going from the normal region to the compressed one across the line of sharp compression, but not blocked when going in the other direction. Again, it is known that in the coelenterates conduction is possible in any direction along the nerves, which were long regarded as a true net or syncytium (119). Recent evidence (31) indicates that even in these animals there exist many synapses between the individual neurons, but axons and dendrites are morphologically quite similar. It would seem that the presence or absence of a transverse synaptic membrane is quite immaterial; as long as the nerve processes

meeting each other at this point are alike in structure the impulse may travel from either one to the other. In the vertebrate nervous system, where irreversible conduction is the rule, there is usually a marked difference between the axon and dendrite meeting each other in the ordinary type of synapse; the axon being normally thin and fairly smooth, the dendrite thick and thorny (23, 83). In such an arrangement, the nerve impulse might be expected to go from the thin to the thick fiber but not in the reverse direction.

It must be noted that the chemical and physical theories together account for all the major properties of reflex conduction, but neither one alone is able to do so satisfactorily. The physical theory, especially, had difficulty in accounting for delayed and prolonged motor effects, since the stimuli involved are all action potentials of short duration. The recent findings (67) that these potentials may last for minutes may remove some of these difficulties.

Conduction from sensory ending to nerve fiber or from nerve fiber to effector also involves the transmission of excitation across a cell junction. It has usually been assumed that similar relations hold in these transmission regions as in a synapse. The particular complex structures of the different types of sensory endings cannot yet be successfully related to their specific functions, but certain characteristics common to them all cannot be without significance. Thus, in all cases, the nerve fiber loses its myelin sheath at a greater or lesser distance from the end organ, and in the end organ proper the simple round axis cylinder may undergo a bewildering variety of divisions, coilings, swellings and the like (114). Common to all these is the establishment of a relatively large surface at the receptive end of a fiber. This increased surface must lead, in terms of our concept of nerve excitation, to a great reduction

in the threshold for excitation, and it is in just such a lowering of threshold that the end organs express their function. In the case of the end organs, as in that of the synapse, it does not appear difficult to understand transmission, whether or not a membrane is interposed between two reacting cells. The epilemmal and hypolemmal endings in muscle would correspond roughly to synapses with and without interposed membranes, yet there is little doubt that in both cases transmission across the boundary is easily possible.

The definite assignment to specific types of sensory endings of the reception of particular sensations is not yet complete, but a very effective start has recently been made (3, 4, 17). It has been shown, for example, by vital staining of the human conjunctiva that the Krause end-bulbs receive cold sensation (141). Also, it may be pointed out that there is no difficulty in reconciling the all-or-none law for the nerve fiber with the ability to sense gradations of stimuli; for a weak painful stimulus produces a slow succession of impulses in the afferent nerve, whereas a strong stimulus produces more frequent impulses of exactly the same character (3). Here, again, the chemical views of transmission across junctions are useful in interpreting the results. A weak stimulus produces a moderate change which in turn generates few impulses; a stronger stimulus produces a greater change and more rapid discharge.

EXTRA-REFLEX EFFECTS

As it was found with the advance of knowledge that no degree of complication of the properties of the axon would adequately account for the properties of the reflex arc, so it seems not unlikely that the reflex arc is not an adequate mechanism to account for all the phenomena exhibited by the central nervous system. Some other means of influence of one part of the nerv-

ous system by another than in terms of nerve impulses conducted between them is suggested by many facts. For example, the establishment of new reflex paths is itself difficult to explain with our present conceptions. Conditioned reflexes, which are easily established, have been widely studied (122). A dog's salivary gland will secrete as a reflex response to the presence of food in the mouth. This is true for all normal dogs and does not depend on the previous experience of the individual. It is an unconditioned inherited reflex. No normal dog secretes saliva when a bell vibrating a particular note is sounded, but if a dog is fed a number of times just after hearing this particular bell, there is established a new reflex so that the ringing of the bell is now an adequate stimulus to salivation. This is the conditioned reflex. Obviously, some type of nervous connection between the auditory center and the salivatory nuclei has been established. Since the individual neuron presumably responds in all or none fashion, so that the impulse travelling in any part of it is uninfluenced by its own history, it is hardly conceivable that it should be influenced by its future. That is, auditory impulses coming along the cochlear nerve and ascending in the central nervous system cannot change their path so as to connect with the salivatory centers, or change potential connections to effective ones, simply because these are active, unless there is some new type of influence exerted by the active centers.

Again, there is often seen the histological picture of the connection of many axons with several widely branched dendrites of a single cell (114). The presumption is that these may all simultaneously affect the common cell and there is physiological evidence, in many cases at least, that their effects may be summed. The case of the mitral cell and the glomeruli in the olfactory system (114), where thousands of

fibers reaching a glomerulus are represented by one leaving it, may be mentioned. On the basis of a chemical or an electrical transmission from the telodendrion of one axon to the particular dendrite in its neighborhood, the response of the cell as a unit to the summed action of many axons on separate dendrites cannot easily be explained.

A still more striking indication of the limitations of the simple reflex concept is seen in the synchronous discharge of groups of nerve cells. In the retina, for example, with millions of receptive endings and of conducting fibers, there exists very sharp discrimination. An object whose image falls on a group of cones can be recognized in consciousness in terms of the number and position of the cones stimulated. If electrodes are placed on the optic nerve while connected with the retina and luminous objects of any size or shape are placed in front of the eye, the activity of the various nerve fibers can be observed in terms of action potentials (7). When a few fibers are excited by a small object each one sends out a series of rhythmical impulses quite independent, in time, of the discharges of any other nerve fiber, so that the total effect is an irregular electrical hodge-podge of potential changes. When a great many fibers are excited by a large object, again each one discharges at its own tempo, and this remains true when nearly all of the retina is illuminated, with only a small darkened region left. When, however, the entire retina is evenly illuminated there suddenly appears a new effect. The individual fibers are no longer carrying impulses at independent rates and times, but the whole group rapidly falls into line so that the discharge in thousands of fibers is timed as if it were one (7, 57). This synchronism is so exact that it is difficult to believe nerve impulses travelling over connecting fibers (which might

conceivably carry to all cells simultaneously the stimulus to discharge) would reach all at once, and even if they did, the absence of synchronism when less than all is illuminated is then impossible of explanation. During respiration, impulses originating in the respiratory center travel down the thousands of fibers in the phrenic nerve and produce a contraction of the diaphragm. Here it is found that during deep inspiration the impulses in all fibers are timed together, so that the nerve cells in the center must have discharged together as a multiple unit (5, 60).

Other evidence comes from the psychological field. An acquired response to a particular stimulus pattern is not dependent on the actual sense organs stimulated and their central connections (97, 106). A complicated figure seen only with one eye is at once recognized and responded to when seen with the other. Lashley (106) has found that the ability of rats to learn or retain successful maze habits depends on the mass of the cerebral cortex. Destruction of brain tissue leads to loss of ability proportional to the extent of the injury. Extensive linear cuts causing little actual loss of tissue but great interference with conduction paths, on the contrary, have little effect. Learning thus appears to depend on some kind of mass integration of the activity of large numbers of neurones; and, of course, all normal subjective experience indicates a unity which is apparently inexplicable in terms of separate impulses rushing along innumerable fibers from cell to cell of the brain.

Finally Coghill's (38) work on amblystoma larvae, showing, during development, the successive crystallization of unit reflexes out of a homogeneous response background is in line with the above mentioned material.

It is not yet known what type of mechanism, aside from the passage of nerve im-

pulses, may be held responsible for these phenomena, but the possibility certainly exists that regional potential changes enter into it. It will be recalled that an active cell develops a negative potential in relation to resting regions; this is true for the nerve fiber and, possibly, for the nerve cell to a greater degree. Also, the sensitivity to stimulation and the type of response of a nerve fiber can be modified by passing electric currents through it, quite aside from their ability to excite it directly (25, 125). In the cases discussed it will be seen that the activity of a large number of cells at approximately the same time would produce potential changes of a whole region which, in turn, might modify the sensitivity of other cells and tend to bring the entire group into synchrony.

There is at least one other situation in regard to the nervous system where potential differences seem to play a morphologic rôle. The processes of the neuroblasts, during the original histogenesis of the nervous system, grow in quite different directions and, in general, seem to develop towards actively growing regions of the body. The expression "neurobiotaxis" has been used to designate this phenomenon (11), which resolves itself essentially into the tendency of nerve fibers to grow in the direction of a negative potential (37, 91).

These, then, are a few indications of how nerve function may be viewed in terms of nerve structure and what the structure may mean functionally. It must be recognized that many of the relations suggested, especially in the second and third parts of this paper, are pure (though not gratuitous) hypotheses. They may all be quite incorrect. The purpose in presenting them is largely to stimulate inquiry and to give meaning to some of the, superficially unimportant, structural details of nerve. Only by the simultaneous pursuit of struc-

tural and functional facts and their close correlation will many of the problems raised here be finally answered.

This article is the outgrowth of an effort to indicate to students of histology the functional significance of

nerve structure, as described in Maximow's Histology. This was originally requested by Professors W. Bloom and C. J. Herrick, editors. Literature since April, 1930, when this article was submitted, is not considered, though certain references have been brought up to date.

LIST OF LITERATURE

- (1) ADRIAN, E. D. 1914. The all-or-none principle in nerve. *Jour. Physiol.*, 47, 460.
- (2) ———. 1922. The relation between the stimulus and the electric response in a single muscle fibre. *Arch. Néerland. de Physiol.*, 7, 332.
- (3) ———. 1928. The Basis of Sensation; The Action of the Sense Organs. W. W. Norton & Co., New York.
- (4) ———. 1930. The mechanism of the sense organs. *Physiol. Reviews*, 10, 336.
- (5) ADRIAN, E. D., and D. W. BRONK. 1928. The discharge of impulses in motor nerve fibres. I. Impulses in single fibres of the phrenic nerve. *Jour. Physiol.*, 66, 81.
- (6) ADRIAN, E. D., and K. LUCAS. 1912. On the summation of propagated disturbances in nerve and muscle. *Jour. Physiol.*, 44, 68.
- (7) ADRIAN, E. D., and R. MATHEWS. 1928. The action of light on the eye. III. The interaction of retinal neurones. *Jour. Physiol.*, 65, 273.
- (8) ADRIAN, E. D., and Y. ZOTTERMAN. 1926. The impulses produced by sensory nerve endings. II. The response of a single end organ. *Jour. Physiol.*, 61, 151.
- (9) AMBERSON, W. R., and A. C. DOWNING. 1929. On the form of the action potential wave in nerve. *Jour. Physiol.*, 68, 19.
- (10) ANGULO Y GONZALES, A. W. 1929. Is myelogeny an absolute index of behavioral capability? *Jour. Comp. Neurol.*, 48, 459.
- (11) ARIËN KAPPERS, C. U. 1917. Further contributions on neurobiotaxis. IX. An attempt to compare the phenomena of taxis and tropism. The dynamic polarization of the neurone. *Jour. Comp. Neurol.*, 27, 261.
- (12) ASHMAN, R., and R. HAFKESBRING. 1929. Unidirectional block in heart muscle. *Am. Jour. Physiol.*, 90, 269.
- (13) AUERBACH, L. 1927. Das histologische Substrat des polarisierten Nerven. *Zeit. f. Zellforsch. u. Mikros. Anat.*, 5, 386.
- (14) VON BAEYER, H. 1903. Das Sauerstoff Bedürfnis des Nerven. *Zeit. f. allgem. Physiol.*, 2, 169.
- (15) BAILEY, P. and H. CUSHING. 1926. A Classification of the Tumors of the Glioma Group on a Histogenetic Basis, with a Correlated Study of Prognosis. Lippincott, Philadelphia.
- (16) BARTELMEZ, G. W. 1915. Mauthner's cell and the nucleus motorius tegmenti. *J. Comp. Neur.*, 25, 87.
- (17) BAZETT, H. C., B. McGLONE, and R. J. BROCKLEHURST. 1930. The temperature changes in the tissues which accompany temperature sensations. *Jour. Physiol.*, 69, 88.
- (18) BELL, CHARLES. 1811. "An idea of a new anatomy of the brain, submitted for the observation of the author's friends." Quoted from J. Müller, *Elements of Physiology*, Taylor & Walton, London. 1837.
- (19) BERITOFF, J. 1929. On the conduction time of the nervous impulses through the central nervous system. *Am. Jour. Physiol.*, 90, 281.
- (20) BERNSTEIN, J. 1871. Untersuchungen über den Erregungsvorgang im Nerven und Muskelsysteme. C. Winter, Heidelberg.
- (21) BETHE, A. 1898. Das Zentralnervensystem von *Carcinus maenas*. Ein anatomisch-physiologischer Versuch. *Arch. f. mikros. Anat.*, 51, 382.
- (22) ———. 1903. Allgemeine Anatomie und Physiologie des Nervensystems. Thieme, Leipzig.
- (23) BIELSCHOWSKY, M. 1928. *Handb. d. mikros. Anat.*, Vol. 4, p. 99. J. Springer, Berlin.
- (24) BISHOP, G. H. 1928. The effect of nerve reactance on the threshold of nerve during galvanic current flow. *Am. Jour. Physiol.*, 85, 417.
- (25) BISHOP, G. H., and J. ERLANGER. 1926. The effects of polarization upon the activity of vertebrate nerve. *Am. Jour. Physiol.*, 78, 630.
- (26) BISHOP, G. H., J. ERLANGER and H. S. GASSER. 1926. Distortion of action potentials as recorded from the nerve surface. *Am. Jour. Physiol.*, 78, 592.

- (27) BOYCOTT, A. E. 1899. Note on the muscular response to two stimuli of the sciatic nerve (frog). *Jour. Physiol.*, 24, 144.
- (28) ———. 1902. On the influence of temperature on the conductivity of nerve. *Jour. Physiol.*, 27, 488.
- (29) ———. 1904. On the number of nodes of Ranvier in different stages of the growth of nerve fibres in the frog. *Jour. Physiol.*, 30, 370.
- (30) BOYD, T. E., and R. W. GERARD. 1930. The effect of prolonged activity on the irritability of medullated nerve. *Am. Jour. Physiol.*, 92, 656.
- (31) BOZLER, E. 1927. Untersuchungen über das Nervensystem der Coelenteraten. I. Kontinuität oder Kontakt zwischen den Nervenzellen. *Zeit. Zellforsch.*, 5, 244.
- (32) ———. 1927. Untersuchungen über das Nervensystem der Coelenteraten. II. Über die Structur der Ganglienzellen und die Function der Neurofibrillen nach Lebensuntersuchungen. *Zeit. vergl. Physiol.*, 6, 255.
- (33) BRAMWELL, J. C., and K. LUCAS. 1911. On the relation of the refractory period to the propagated disturbance in nerve. *Jour. Physiol.*, 42, 495.
- (34) BREMER, F., and P. RYLANT. 1925. Nouvelles recherches sur le mécanisme de l'action de la strychnine sur le système nerveux central. *Comp. Rend. Soc. Biol.*, 92, 199.
- (35) BÜHLER, K. 1905. Über den Einfluss tiefer Temperaturen auf die Leitfähigkeit des motorischen Froshnerven. *Arch. f. Physiol.*, p. 239.
- (36) CARLSON, A. J. 1910-11. The effects of stretching the nerve on the rate of conduction of the nervous impulse. *Am. Jour. Physiol.*, 27, 323.
- (37) CHILD, C. M. 1921. *The Origin and Development of the Nervous System*. The University of Chicago Press, Chicago.
- (38) COGHILL, G. E. 1929. *Anatomy and the Problem of Behavior*. Camb. Univ. Press, London.
- (39) COOPER, S., and E. D. ADRIAN. 1924. The electric response in reflex contractions of spinal and decerebrate preparations. *Proc. Roy. Soc., B.*, 96, 243.
- (40) COOPER, S., and D. DENNY-BROWN. 1927. Responses to stimulation of the motor areas of the cerebral cortex. *Proc. Roy. Soc. B.*, 102, 222.
- (41) DAVIS, H. 1926. The conduction of the nerve impulse. *Physiol. Rev.*, 6, 547.
- (42) DAVIS, H., A. FORBES, D. BRUNSWICK and A. McH. HOPKINS. 1926. Studies of the nerve impulse. II. The question of decrement. *Am. Jour. Physiol.*, 76, 448.
- (43) DE RENYI, G. ST. 1929. The structure of cells in tissues as revealed by microdissection. IV. Observations on neurofibrils in living nervous tissue of the lobster (*Homarus americanus*). *J. Comp. Neurol.*, 48, 441.
- (44) DOWNING, A. C., R. W. GERARD, and A. V. HILL. 1926. The heat production of nerve. *Proc. Roy. Soc., B.*, 100, 223.
- (45) DUBOIS REYMOND, E. 1848. *Untersuchungen über thierische Electricität*. Reimer, Berlin.
- (46) ERLANGER, J. 1927. The interpretation of the action potential in cutaneous and muscle nerves. *Am. Jour. Physiol.*, 82, 644.
- (47) ERLANGER, J., G. H. BISHOP, and H. S. GASSER. 1926. The action potential waves transmitted between the sciatic nerve and its spinal roots. *Am. Jour. Physiol.*, 78, 574.
- (48) ERLANGER, J., and H. S. GASSER. 1924. The compound nature of the action current of nerve disclosed by the cathode ray oscillograph. *Am. Jour. Physiol.*, 70, 624.
- (49) ———. 1930. The action potential in fibres of slow conduction in spinal roots and somatic nerves. *Am. Jour. Physiol.*, 92, 43.
- (50) ETTISCH, G., and J. JOACHIMS. 1927. Dunkelfeld-untersuchungen am überlebenden Nerven. *Pflüger's Arch.*, 215, 519.
- (51) FENG, T. P., and R. W. GERARD. 1930. Mechanism of nerve asphyxiation: with a note on the nerve sheath as a diffusion barrier. *Proc. Soc. Exp. Biol. and Med.*, 27, 1073.
- (52) FENN, W. O. 1927. The oxygen consumption of frog nerve during stimulation. *Jour. Gen. Physiol.*, 10, 767.
- (53) FORBES, A. 1922. The interpretation of spinal reflexes in terms of present knowledge of nerve conduction. *Physiol. Rev.*, 2, 361.
- (54) FORBES, A., and A. GREGG. 1915. Electrical studies in mammalian reflexes. I. The flexion reflex. *Am. Jour. Physiol.*, 37, 118.
- (55) FORBES, A., and L. H. RICE. 1929. Quantitative studies of the nerve impulse. IV. Fatigue in peripheral nerve. *Am. Jour. Physiol.*, 90, 119.
- (56) FOSTER, M. 1901. *History of Physiology*. Cambridge University Press, London.
- (57) FROHLICH, F. W. 1913. Beiträge zur allgemeinen Physiologie der Sinnesorgane. *Zeit. f. Sinnesphysiol.*, 48, 28. Weitere Beiträge zur allgemeinen Physiologie der Sinnesorgane. *Ibid.*, p. 354.

- (58) FULTON, J. F. 1926. Muscular Action and the Reflex Control of Movement. Williams & Wilkins, Baltimore.
- (59) FURUSAWA, K. 1929. The depolarization of crustacean nerve by stimulation or oxygen want. *Jour. Physiol.*, 67, 325.
- (60) GASSER, H. S. 1928. The analysis of individual waves in the phrenic electroneurogram. *Am. Jour. Physiol.*, 84, 569.
- (61) GASSER, H. S., and J. ERLANGER. 1927. The rôle played by the sizes of the constituent fibres of a nerve trunk in determining the form of the action potential wave. *Am. Jour. Physiol.*, 80, 522.
- (62) ———. 1929. The rôle of fibre size in the establishment of a nerve block by pressure or cocaine. *Am. Jour. Physiol.*, 88, 581.
- (63) GERARD, M. W. 1923. Afferent impulses of the trigeminal nerve. The intramedullary course of the painful, thermal and tactile impulses. *Arch. Neurol. & Psych.*, 9, 308.
- (64) GERARD, R. W. 1927. The two phases of heat production of nerve. *Jour. Physiol.*, 62, 349.
- (64a) ———. 1927. Studies on nerve metabolism. I. The influence of oxygen lack on heat production and action current. *Jour. Physiol.*, 63, 280.
- (65) ———. 1927. Studies on nerve metabolism. II. Respiration in oxygen and nitrogen. *Am. Jour. Physiol.*, 82, 381.
- (66) ———. 1928. Der Stoffwechsel des Nerven. *Die Medizinische Welt*, 36.
- (67) ———. 1930. Delayed action potentials in nerve. *Am. Jour. Physiol.*, 93, 337.
- (68) GERARD, R. W., and A. FORBES. 1928. A note on action currents and "equilibration" in the cat's peroneal nerve. *Am. Jour. Physiol.*, 86, 178.
- (69) ———. 1928. "Fatigue" of the flexion reflex. *Am. Jour. Physiol.*, 86, 186.
- (70) GERARD, R. W., and R. GRINKER. 1931. Repair in the immature mammalian central nervous system. *Arch. Neurol. and Psych.* In press.
- (71) GERARD, R. W., A. V. HILL, and Y. ZOTTERMAN. 1927. The effect of frequency of stimulation on the heat production of nerve. *Jour. Physiol.*, 63, 130.
- (72) GERARD, R. W., and O. MEYERHOF. 1927. Untersuchungen über den Stoffwechsel des Nerven. III. Chemismus und Intermediärprozesse. *Biochem. Zeit.*, 191, 125.
- (73) GERARD, R. W., and N. TUPIKOW. 1930. Creatine in medullated nerve. *Proc. Soc. Exp. Biol. & Med.*, 28, 360.
- (74) GERARD, R. W., and J. WALLÉN. 1929. Studies on nerve metabolism. V. Phosphates. *Am. Jour. Physiol.*, 89, 108.
- (75) GOLDSCHMIDT, R. 1910. Sind die Neurofibrillen das leitende Element des Nervensystems? *Sitzungsbr. Ges. Morph. u. Physiol. Münch.*, 26, 28.
- (76) GOTCH, F., and G. J. BURCH. 1899. The electrical response of nerve to two stimuli. *Jour. Physiol.*, 24, 410.
- (77) HAIDENHAIN, M. 1911. Plasma und Zelle, in Bardeleben's Handbuch, Fischer, Jena.
- (78) See HALLER, *Elementa physiologiae corporis humani*. IV. p. 269. Lausannae, Sumpstibus M. & M. Bousquet et Sociorum, 1757-1778.
- (79) HATAI, S. 1910. On the length of the internodes in the sciatic nerve of *Rana temporaria* (fusca) and *Rana pipiens*: being a re-examination by biometric methods of the data studied by Boycott ('04) and Takahashi ('08). *Jour. Neurol. & Psych.*, 20, 19.
- (80) HEINBECKER, P. 1930. Reported at Am. Physiol. Soc. See Bishop and Heinbecker. 1930. Differentiation of axon types in visceral nerves by means of the potential record. *Am. Jour. Physiol.*, 94, 170.
- (81) ———. 1930. The potential analysis of the turtle and cat sympathetic and vagal nerve trunks. *Am. Jour. Physiol.*, 93, 284.
- (82) HEINBECKER, P., and G. H. BISHOP. 1929. Differentiation between types of fibres in certain components of involuntary nervous system. *Proc. Soc. Exp. Biol. & Med.*, 26, 645.
- (83) HELD, H. 1897. Beiträge zur Struktur und ihre Fortsetzung. *His Arch.*, p. 204.
- (84) ———. 1929. Die Lehre von den Neuronen und vom Neuronensyncytium und ihr heutigen Stand. *Fortsch. d. Naturwissensch. Forschung* (Abderhalden) Berlin.
- (85) VON HELMHOLTZ, H. 1850. Vorläufiger Bericht über die Fortpflanzungsgeschwindigkeit der Nervenreizung. *Arch. f. Anat. u. Physiol.*, p. 71. Messungen über den zeitlichen Verlauf der Zuckung animalischer Muskeln und die Fortpflanzungsgeschwindigkeit der Reizung in den Nerven. *Ibid.*, p. 276.
- (86) HELMHOLTZ, H., and BAXT. 1867. Monatsber. d. Berliner Acad., p. 228. (Quoted from L. Hermann, *Handbuch der Physiol.*, Vol. 2, 1879. Vogel, Leipzig.)

- (86a) HERRICK, C. J. 1927. Introduction to Neurology. W. B. Saunders, Philadelphia.
- (87) HERZEN, A. 1885. Über die Spaltung des Temperatursinnes in zwei gesonderte Sinne. *Pflüger's Arch.*, 38, 93.
- (88) HOLMES, E. G., and R. W. GERARD. 1929. Studies on nerve metabolism. IV. Carbohydrate metabolism of resting mammalian nerve. *Biochem. Jour.*, 23, 738.
- (89) HOLMES, E. G., R. W. GERARD, and E. I. SOLOMON. 1930. Studies on nerve metabolism. VI. The carbohydrate metabolism of active nerve. *Am. Jour. Physiol.*, 93, 342.
- (90) HOWELL, W. H., and G. C. HUBER. 1892. A physiological, histological and clinical study of the degeneration and regeneration in peripheral nerve fibers after severance of their connections with the nerve centers. *Jour. Physiol.*, 13, 335.
- (91) INGVAR, S. 1920. Reaction of cells to the galvanic current in tissue cultures. *Proc. Soc. Exp. Biol. & Med.*, 17, 198.
- (92) JENKINS, O. P., and A. J. CARLSON. 1904. Physiological evidence of the fluidity of the conducting substance in the pedal nerve of the slug—*Ariolimax columbianus*. *Jour. Comp. Neurol.*, 14, 85.
- (93) JOLLY, W. A. 1910. On the latency of the knee jerk. *Quart. J. Exp. Physiol.*, 4, 67.
- (94) KATO, G. 1924. The Theory of Decrementless Conduction in Narcotized Region of Nerve. Seibunsha Co., Tokio, Nankodo.
- (95) KATSUMA, S. 1927. Über Wirkungen des konstanten Stroms auf das mikroskopische Bild des Nerven. *Pflügers Arch.*, 227, 279.
- (96) KISS, F., and P. V. MIHALIK. 1928. Über die Zusammensetzung der peripherischen Nerven und den Zusammenhang zwischen Morphologie und Function der peripherischen Nervenfasern. *Zeit. f. Anat. u. Entwicklungsgesch.*, 88, 112.
- (97) KÖHLER, W. 1929. Gestalt Psychology. Liveright, N. Y.
- (98) KRONENBERG. Plexuum nervorum structura et virtutes, Berol. 1836. Quoted from J. Müller, *Elements of Physiology*, Taylor and Walton, London, 1837.
- (99) KÜHNE, W. 1859. Untersuchungen über Bewegungen und Veränderungen der kontraktilen Substanzen. *Arch. f. Anat. u. Physiol.*, p. 564.
- (100) LAPICQUE, L. 1926. L'Excitation en Fonction du Temps. Les Presses Universitaires de France. Paris.
- (101) LAPICQUE, L. and M. 1908. Sur le mecanisme de la curarization. *C. R. de Biol.*, 65, 733.
- (102) ———. 1925. Nouvelle demonstration de l'égalité des chronaxies entre le muscle strié et son nerf moteur. *Ibid.*, 180, 1056.
- (103) LAPICQUE, L., and R. LEGENDRE. 1913. Relation entre le diamètre des fibres nerveuses et leur rapidité fonctionnelle. *C. R. Acad. Sc.*, 157, 1163.
- (104) ———. 1922. Altérations des fibres nerveuses myéliniques sous l'action des anesthésiques et de divers poisons nerveux. *Jour. Physiol. Path. Gén.*, 21, 163.
- (105) LAPICQUE, L., and H. LAUGIER. 1910. Modifications dans l'excitabilité du nerf par une striction progressive. *C. R. Soc. Biol.*, 69, 46.
- (106) LASHLEY, K. S. 1929. Brain Mechanisms and Intelligence. Univ. of Chicago Press, Chicago.
- (107) LEVIN, A. 1927. Fatigue, retention of action current and recovery in crustacean nerve. *Jour. Physiol.*, 63, 113.
- (108) LIDDELL, E. G. T., and C. S. SHERRINGTON. 1923. Stimulus rhythm in reflex tetanic contraction. *Proc. Roy. Soc. B.*, 95, 142. A comparison between certain features of the spinal flexor reflex and the decerebrate extensor reflex respectively. *Ibid.*, p. 299.
- (109) LILLIE, R. S. 1923. Protoplasmic Action and Nervous Action. University of Chicago Press, Chicago.
- (110) ———. 1925. Factors affecting transmission and recovery in the passive iron wire nerve model. *Jour. Gen. Physiol.*, 7, 473.
- (111) LUCAS, K. 1917. The Conduction of the Nervous Impulse. Longmans, Green & Co., London, N. Y.
- (112) MAGENDIE, M. 1822. *Jour. de Physiol.*, 2, 276. Quoted from J. Müller, *Elements of Physiology*, Taylor & Walton, London, 1837.
- (113) MATHEWS, B. H. C. 1929. Specific nerve impulses. *Jour. Physiol.*, 67, 169.
- (114) MAXIMOW, A., and W. BLOOM. 1930. A Textbook of Histology. W. B. Saunders & Co., Philadelphia.
- (115) MCGINTY, D. A., and R. GEBELL. 1925. On the chemical regulation of respiration. II. A quantitative study of the accumulation of lactic acid in the isolated brain during anaerobic conditions and the rôle of lactic acid as a continuous regulator of respiration. *Am. Jour. Physiol.*, 75, 70.

- (116) MEEK, W. J., and W. E. LEEPER. 1911. Effects of pressure on conductivity in nerve and muscle. *Am. Jour. Physiol.*, 27, 308.
- (117) MOTT, F. W., and W. D. HALLIBURTON. 1901. The chemistry of nerve degeneration. *Phil. Trans. B.*, 194, 437.
- (118) NAGEOTTE, J. 1922. L'organisation de la matière dans ses rapports avec la vie. F. Alcan, Paris.
- (119) PARKER, G. H. 1919. The Elementary Nervous System. Lippincott, Philadelphia.
- (120) ———. 1925. The production of carbon dioxide by nerve. *Jour. Gen. Physiol.*, 7, 641. The excretion of carbon dioxide by frog nerve. *Ibid.*, 8, 21.
- (121) ———. 1929. The neurofibril hypothesis. *QUART. REV. BIOL.*, 4, 155.
- (122) PAVLOV, I. P. 1927. Conditioned reflexes. Oxford Press, London.
- (123) PETERFI, T. 1929. In *Handb. d. normalen u. pathol. Physiol.*, Vol. 9. Springer, Berlin. Das leitende Element.
- (124) ———. Verbal communication.
- (125) PFLÜGER, E. 1859. Untersuchungen über die Physiologie des Electrotonus. Hirschwald, Berlin. See p. 453.
- (126) PIPER, H. E. 1912. Electrophysiologie menschlicher Muskeln. Springer, Berlin.
- (127) RANSON, S. W. 1911. Non-medullated nerve fibres in the spinal nerves. *Am. Jour. Anat.*, 12, 67.
- (128) ———. 1915. Unmyelinated nerve fibres as conductors of protopathic sensation. *Brain*, 38, 381.
- (129) ———. 1927. The Anatomy of the Nervous System. 2nd edition, p. 47. W. B. Saunders & Co., Philadelphia.
- (130) RICE, L. H., and H. DAVIS. 1928. Uniformity of narcosis in peripheral nerve. *Am. Jour. Physiol.*, 87, 73.
- (131) RUSHTON, W. A. H. 1927. The effect upon the threshold for nervous excitation of the length of nerve exposed, and the angle between current and nerve. *Jour. Physiol.*, 63, 357.
- (132) ———. 1930. Excitable substances in the nerve-muscle complex. *Jour. Physiol.*, 70, 317.
- (133) SCHÄFER, E. A. 1912. *Quain's Anat.*, 2, 281. Longmans, Green & Co.
- (134) SCHMIDT, C. F. 1928. The influence of cerebral blood flow on respiration. II. The gaseous metabolism of the brain. *Am. Jour. Physiol.*, 84, 223.
- (135) SCHWARTZ, A. 1911. Über die Beeinflussung der primären Farbbarkeit und der Leitungsfähigkeit des polarisierten Nerven durch die den Strom zuführenden Ionen. *Pflüger's Arch.*, 138, 487.
- (136) SHERRINGTON, C. S. 1906. The Integrative Action of the Nervous System. Yale University Press, New Haven.
- (137) ———. 1925. Remarks on some aspects of reflex inhibition. *Proc. Roy. Soc. B.*, 97, 519.
- (138) STEFL, J. 1928. Über die Veränderungen der Nervenstruktur durch den Wechselstrom. *Pflüger's Arch.*, 221, 150.
- (139) STEINACH, E. 1899. Über die centripetale Erregungsleitung im Bereiche des Spinal-gangliens. *Pflüger's Arch.*, 78, 291.
- (140) STOPFORD, J. S. B. 1924-25. The function of the spinal nucleus of the trigeminal nerve. *Jour. Anat.*, 59, 120.
- (141) STRUGHOLD, H., and M. KARBE. 1925. Vitale Färbung des Auges und experimentelle Untersuchung der gefärbten Nervenelemente. *Zeit. f. Biol.*, 83, 297.
- (142) STUBBEL, H. 1913. Morphologische Veränderungen des gereizten Nerven. II. *Pflüger's Arch.*, 153, 111.
- (143) SYMES, W. L., and V. H. VELEY. 1910-11. The effect of some local anesthetics on nerve. *Proc. Roy. Soc. B.*, 83, 421.
- (144) SZPILMAN, J., and B. LUCHSINGER. 1881. Zur Beziehung von Leitungs- und Erregungsvermögen der Nervenfasern. *Pflüger's Arch.*, 24, 347.
- (145) TAKAHASHI, K. 1908. Some conditions which determine the length of the internodes found on the nerve fibres of the Leopard Frog, *Rana pipiens*. *Jour. Comp. Neurol. & Psych.*, 18, 167.
- (146) TASHIRO, S. 1917. A Chemical Sign of Life. University of Chicago Press, Chicago.
- (147) THÖLE, DR. 1912. Über Jucken und Kitzeln in Beziehung zu Schmerzgefühl und Tastempfindung. *Neurol. Zentralbl.*, 31, 610.
- (148) WEBER, E. H. Annot. Anat. et Physiol. Quoted from J. Müller, *Elements of Physiology*, Taylor & Walton, London. 1837.



FACTS AND THEORIES OF BIRD FLIGHT

By LUCIEN H. WARNER

White Plains, N. Y.

BESIDES the birds and their immediate ancestors, only certain insects and bats have succeeded in solving the problems of true flight. Many other forms, having derived sufficient momentum from another medium, can glide through the air for a considerable distance. True flight adds to this the ability of maintaining both altitude and speed by displacement of the air itself. Much has been written of the origin of bird flight but little is definitely known. It may be that it developed from the gliding leaps of the tree-living ancestors of the modern bird. Certain amphibians and mammals incapable of true flight but capable of gliding have been observed to terminate long glides with an upward turn. This sudden gain of altitude takes them up to a selected landing place, but at the cost of their momentum. It is quite conceivable that a successful glider would lengthen the span of flights by vigorous downward displacement of the air with movements of its gliding surfaces. The more generally accepted notion, however, is that the original flyers launched themselves into the air not from treetops but from the ground. It is assumed that these forms were capable of rapid bipedal locomotion which served no doubt as a means of escape. The forelimbs being released could, in moments of need for great speed, become primitive gliding surfaces, by means of which the animal's long strides could be lengthened. This view is sup-

ported by the discovery of extinct forms (Ornithischia) which resemble this hypothetical bird ancestor. Such forms may or may not have been close to the line of descent of the birds. It is not impossible that flight was achieved independently by several different reptilian forms, and that some approached flight by one means, some by another.

Thomson (25) has compiled a list of preconditions of flight, i.e., characteristics which it is assumed an organism must have possessed before it was capable of even brief sustained flight. To this he adds a list of accessory adaptations supposed to have occurred subsequent to the beginnings of flight. Inasmuch as the exact sequence of development of such characteristics is largely a matter of speculation and since our chief interest is in bird flight as it occurs to-day, we shall here make no effort to discuss the bird's characteristics in the order of their evolutionary origin.

THE POWER : WEIGHT RATIO

The solution of the problem of true flight presupposes the fulfillment of two conditions. First, the value of the following fraction must exceed a certain minimum:

$$\frac{\text{The power which can be developed by the organism}}{\text{The weight of the organism}}$$

Secondly, the organism must be capable of maintaining the quotient above such a minimum for more than a brief length

of time if flight over a distance appreciably greater than a jump and a glide is to be achieved. It is probable that in very few vertebrates besides birds would this quotient be adequate, even supposing that such forms possessed the means of applying their power efficiently. Most of the characteristics which are responsible for the high quotient in birds are classified by Thomson as "preconditions."

Considering first the numerator of our fraction we must mention the powerful musculature of the typical bird. Those muscles involved in flying, and especially the pectoral muscles which depress the wing, are highly developed. In most birds these muscles compose over one-sixth of the total weight and in certain pigeons they equal in weight the remainder of the bird. If to these huge pectoral muscles we add the other flying muscles and the tendons, bones and feathers directly involved in flight it will be seen that the bird is composed mostly of flying machinery. The remainder of the animal might be considered subservient, being largely organs for the guidance of this machinery and for its nourishment. This last function is of course, most essential. Except in those birds which can, on occasion, soar, sustained flight involves continuous muscle exertion, each individual muscle having but brief, rhythmic periods of relaxation. This would be impossible were it not for the efficient circulatory and respiratory apparatus for the conveyance of nourishment to the muscle tissues and the removal of waste products. The blood of birds contains a larger proportion of red corpuscles than that of any other animal. The heart is powerful and in it we find a completely divided ventricle. Furthermore, the arrangement of the blood vessels is such that there is no admixture of pure and impure

blood. In no forms below the birds is this goal attained, although it is approached in some of the higher reptiles. Excellent digestion and respiration maintain the purity of the blood. Examination of bird faeces indicates that birds utilize a far higher proportion of the nutritive value of their food than do mammals, for example. The lungs communicate with air-sacs which are not confined to the thoracic region but often penetrate remote parts of the body, entering bones of the skull, wings and sometimes even the legs and toes. It is said (3) that a bird with a broken wing can breathe through the splintered end of this hollow bone when its windpipe is completely choked with blood. While the air-sacs are important chiefly in connection with temperature regulation it is claimed that they also facilitate respiration. There may be little interchange of gases in them but they assist in the ventilation of the lungs, creating what has been termed a "double-tide" of respiration. Equally important is the relationship of the flying movements to the respiratory movements. The lungs are inexpandible; when relaxed they are filled. The active part of respiration is exhalation caused by compression of the ribs and breastbone, which surround the lungs. The wing movements involve such compression. Thus the more rapidly the wings are moved, the greater the amount of air forced in and out of the lungs. It can be seen that the bird is far less likely to get out of breath than is a mammal, which must accomplish locomotion and respiration by two sets of mechanisms operating separately though of necessity simultaneously. Finally, the bird's capacity for maintaining a constant body temperature results in an efficient operation of the metabolic processes unaffected by fluctuation in environmental tempera-

ture. All these factors and others result in a high rate of metabolism and in the production of great and sustained power.

That the denominator of the fraction, weight, is kept low has already been suggested in our emphasis upon the relatively slight weight of those portions of the animal not immediately involved in locomotion. Surplus weight of all sorts is reduced to a minimum. The body is lean and spare. The reproductive organs are simple and compact and are usually much reduced except during the mating season. The skeletal structure is light, yet strong, largely as a result of fusion of parts. Many individual bones are large, so furnishing ample surface for the adhesions of muscles and tendons and yet they are light, being constructed on the hollow-girder principle. The cross-section of many such bones gives a splendid illustration of economy of material without sacrifice of rigidity. A purposivist should find much pleasure in noting that each bone seems so constructed as to withstand exactly those stresses and strains to which, because of its position and connections, it is subjected.

THE APPLICATION OF POWER TO FLIGHT

But an adequate ratio of power to weight is useless unless that power can be efficiently applied. Obviously, the less efficiently it is applied, the more favorable must be the "power: weight" ratio if flight is to be attained. Probably the most important single item developed by birds in this connection is feathers. True, flight has been achieved by bats without these structures. Nevertheless, feathers, because of their light weight, their impermeability to air, their curvature and general shape, seem to be the ideal material for the construction of planes. Furthermore, a wing which is composed of a number of units, themselves curved

and pliable, may, by alteration of the position of these units, be moulded into varying degrees of both curvature and extension to meet the requirements of shifting air currents. The bird-wing, being strong, light, and capable of almost instantaneous alteration of angle and curvature, is likely to prove superior to any planing surface that man will create. Given two such wings and powerful pectoral muscles for their depression there still must be bases for the anchorage of the muscles and a fulcrum against which the wings can pivot. The keel which is developed from the breastbone fills the former requirement. It is lacking or small only in birds such as the ostrich which no longer use their wings for flying. Its development is retained in those birds which have taken to water and use their wings vigorously in swimming. A rigid fulcrum for the wings is supplied by the fusion of the thoracic vertebrae in all flying birds. We thus have outlined briefly the mechanism whereby the wings are suddenly depressed. This is the fundamental movement in the maintenance of the bird in the air. Obviously the wings must be raised between strokes. This is accomplished by the pectoralis minor, a muscle lying ventral to the breastbone. Its *downward* pull is converted into an *upward* pull upon the wings by means of a tendon extending through an opening at the shoulder joint (which thus functions as a pulley) and out to the upper surface of the wing. Besides the structures mentioned there are, of course, many others concerned in the control of the body during flight. Most of these consist of muscles for the alteration of the tail and head positions and for the alteration in flexion and curvature of the wings. Further conditions facilitating the efficient application of the bird's power in flight relate to the general shape and

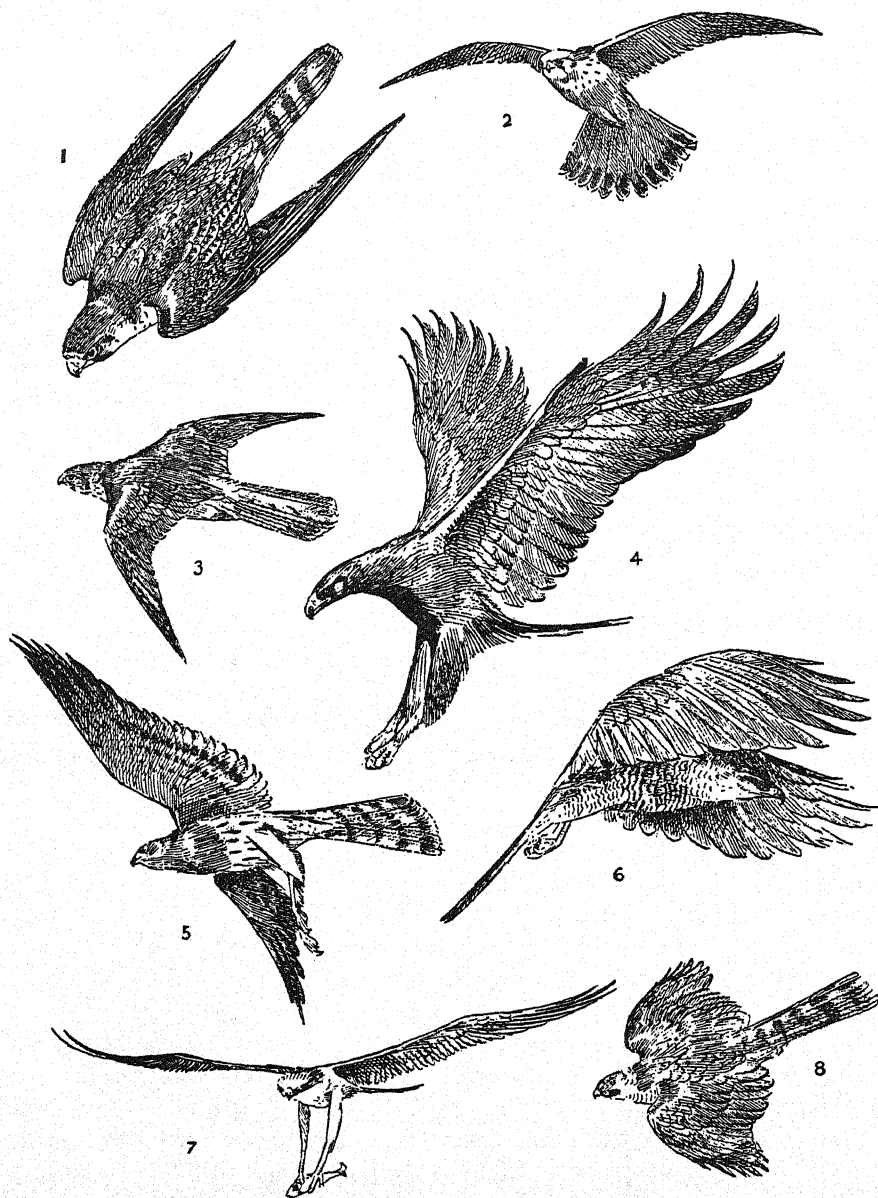
weight distribution of the body. The bird's body is streamlined, as are those of other forms accustomed to float in a fluid medium. The feather covering adds to this effect by filling in the unevennesses of the surface. Prominent irregularities of surface, as, for example, those formed by external ears, are lacking. As compared with its probable reptile-like ancestors, the bird's tail is shortened and its neck lengthened. The effect is to shift the center of balance further forward. The advantage of this is obvious when it is noted that the supporting wings are attached to the anterior portion of the body. A further condition which tends to stabilize the position of the bird when floating on its wings is the ventral location of the heavier organs of digestion and the dorsal position of the lighter organs of respiration. Finally, since the wings are attached to the dorsal portion of the body, it can be seen that, even though a bird were not to make adequate compensatory movements, it would be indeed a capricious wind which could upset it in the air.

SPECIALIZATIONS IN FLIGHT

While the above remarks are applicable to flying birds in general one must not forget that there are wide variations in the structure and in the flight of birds (Figure 1). Only examples of such can be given here. There is great variation in size of the wings. The smaller the bird the larger must be its wing in proportion to its body size. This is because there is a relatively larger proportion of border area in a small wing and this area possesses less lifting value since the air readily slips past it. The lifting value of various points on the wing surface increases with increase in distance from the edge of the wing. Nevertheless, even amongst birds of the same size we find striking difference in the size, and particularly in the length

of the wings. This is usually related to the habitat of the bird. Those living in thicket and forest, like the wren and the pheasant, possess shorter and broader wings, while birds of the open spaces, like gulls and swallows, have long ones. The type of flight depends to a considerable degree upon the amount of effective wing surface. A bird with an abundance of wing surface can afford to flap its wings and glide alternately. Speed is maintained during the glide through loss in altitude. Such a bird can quickly and easily regain the lost altitude. Most of our song birds fly in this fashion. Birds with a smaller wing area in proportion to weight can gain altitude only with difficulty. Having gained it, they prefer to flap their wings continuously rather than to lose it. The grouse and the ducks are examples. The frequency of the wing beat also is related to wing size. Here again there is wide variation, as may be exemplified by the hummingbird at one extreme and the crow at the other. The noise accompanying flight varies from the whistle of the stiff quills of the grouse to the unheard whisper of the downy feathers of the owl.

It can readily be seen that birds cannot be ranked according to their flying ability without taking into consideration the conditions under which flying occurs. No single flying equipment best suits all conditions of wind and calm, of sea and forest, etc. The ability to fly at a great speed or for long distances, to make quick getaways and to dodge and turn with agility, to maintain a constant altitude with a minimum of progression, to dive from heights, these and many other abilities that could be mentioned are so conflicting in their structural requirements that only a few of them are to be found well developed in any one bird. Probably the most striking examples of specializa-



1. PEREGRINE FALCON.
2. KESTREL.
3. MERLIN.
4. GOLDEN EAGLE.

5. MONTAGU'S HARRIER.
6. GOSHAWK.
7. OSPREY.
8. SPARROW HAWK.

FIG. 1. A SUGGESTION OF THE GREAT VARIETY OF FLIGHT IS GAINED BY NOTING THE VARIATION IN SHAPE AND RELATIVE SIZE OF WINGS (After Pycraft)

tion for one type of flying condition at the expense of the capacity to meet other conditions is to be found among the soaring birds. Peerless though they are when in "soarable" air currents, they are helpless under many conditions which would hold no terrors for a more generalized bird. The albatross with slim wings and a wingspan of eleven feet is admirably adapted for soaring on the currents deflected upward by waves. But on those rare occasions when the sea is perfectly calm and there is no wind they cannot rise from the water. Vultures, eagles and other large soaring birds have difficulty in rising in a calm unless they can jump from a branch or other high place and so gain the needed momentum by a loss of altitude. They can rise from the level ground only with difficulty and after an awkward run and leap. It is said that they can be trapped by being enticed into a small yard.

GLIDING

We turn now to the modes of flight. It has been said that they are three in number, gliding, flapping and soaring. Although we shall try to show that there is a fundamental similarity between the first and last of these, we shall, for the sake of clarity, take them up in the order just given.

When any body is dropped its fall is impeded by the resistance of the air through which it passes. This resistance increases (approximately) as the square of its speed. If this body is so shaped that in falling it presents a considerable horizontal surface (for example, a sheet of paper dropped flat) the resistance offered by the air is greatly increased. If this object, which is now really a plane, is dropped with the large surface area not lying exactly in the horizontal plane, but tipped, the resultant resolution of forces causes it to make lateral progress during

the fall. This progress is in the direction of the lower edge of the plane. Providing our plane is so weighted and shaped that it will maintain the same angle with the horizontal throughout the fall it will continue this lateral progression from the time of its release until it lands. The paper gliders cut out by children neatly illustrate this. All flying birds are capable of this form of gliding. Their curved wings function more efficiently than would straight surfaces. They can maintain and even increase lateral speed at the cost of altitude. By altering the angle of the plane, gliding flight is possible without loss of altitude and even with gain of altitude, but at the cost of lateral speed. When this speed is reduced to nil the lifting effect of the plane is entirely lost. These statements refer to flight in a dead calm or in a uniformly moving body of air. The important points are (1) that gliding requires no other wing movement than adjustment to a suitable angle; (2) that gliding involves either loss in altitude, loss in speed or both. It is obvious, then, that prior to gliding a bird must in some way have gained either altitude or speed. Furthermore, the duration of a glide is definitely limited by the altitude or speed gained.

FLAPPING

The second mode of flight is less limited since in this case it is maintained not at the expense of altitude or speed but at the expense of the energy of the bird. The mechanism for wing movement has been discussed above. The strokes of the two wings occur simultaneously. Were they to alternate, as do the legs of a biped in walking, the bird would roll. Although synchronous action avoids this, it results in an undulating flight. However rapid the strokes and however great the momentum of the bird, there is bound to be a

slight loss in altitude on the up-stroke which is quickly compensated for by a gain on the strong down-stroke. In the case of heavy birds the wing movements of which are slow, this rise and fall can easily be observed. The impulse forward results from the angle of the wings, the down pressure being exerted at the forward edges. This mode of locomotion has been compared to the rowing of a boat. It should be observed, however, that the action of the oars serves to send the boat forward but not to keep it afloat. The

to flappers as it is to gliders. The less the speed the more vigorous must the strokes be if they are to have the same effect. It can readily be seen, then, that the most difficult part of flight is the start. If a bird is on the ground and cannot attain speed by dropping a short distance before rising it must leap into the air, perhaps after a run, and flap its wings violently for several strokes to gain such momentum that less vigorous strokes may be effectual. If a pigeon is observed in his take-off, one can see and hear his wing tips strike each

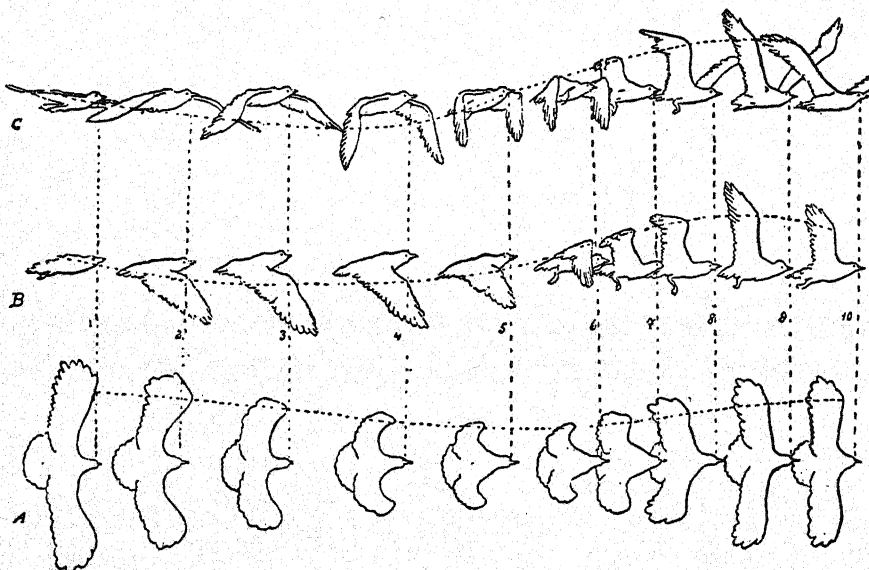


FIG. 2. SUCCESSIVE PHASES OF THE WING STROKE IN THE GULL (After Marcy)

bird depends upon its wings for maintenance of altitude as well as for progress. Headley's description of flying (8) is far better. He says that flying consists of a series of jumps in which the bird uses as the fulcrum for each jump, a column of air. The more support the wing finds in a column of air the longer the "jump" that can be made from it. An important point is that the greater the speed of the bird, the greater the air pressure under the wing, i.e., the greater the support in the air column. Speed is, therefore, as important

other at the top of each stroke, an indication that his strokes are not merely vigorous but as extensive as possible. It has been observed that if a bird in an enclosure is frightened off the ground several times in quick succession it begins to breathe hard, and eventually refuses to take wing. Headley emphasizes the fact that birds appear to prefer to fly in air that has not just been ruffled by another bird. In migration formations each successive bird follows not exactly in the wake of its predecessor but to one side. Presumably,

this is so in order that, for each stroke, the bird will be supplied with a fresh, undisturbed column of air. The hovering in

Motion picture photography has opened the way to analysis of the strokes of the wings. The chief fact revealed is that in

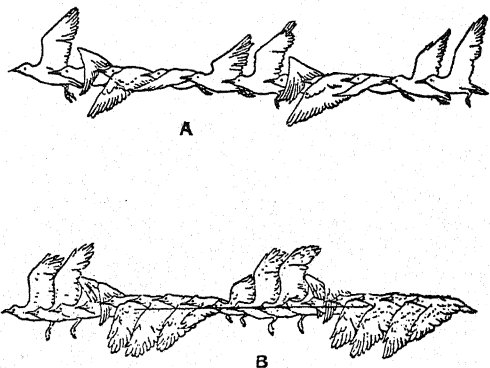


FIG. 3. SUCCESSIVE PHASES OF THE WING STROKE IN THE GULL

A. Twenty-five photographs per second. B. Fifty per second. (After Marey.)

one place which is accomplished by humming-birds, appears to be an example of flight in which a fresh column of air is not supplied for each stroke of the wings. It has been claimed, however, that such



FIG. 4. THE START, A PHOTOGRAPH TAKEN JUST AFTER THE LEAP

Note position of tail and contrast with Figure 5. (After Headley.)

hovering occurs only when there is sufficient wind to supply each stroke with a new column. In any case, only the very strongest flyers are capable of hovering.



FIG. 5. PIGEON ALIGHTING

Note braking by wings and tail, and preparation of feet. (After Headley.)

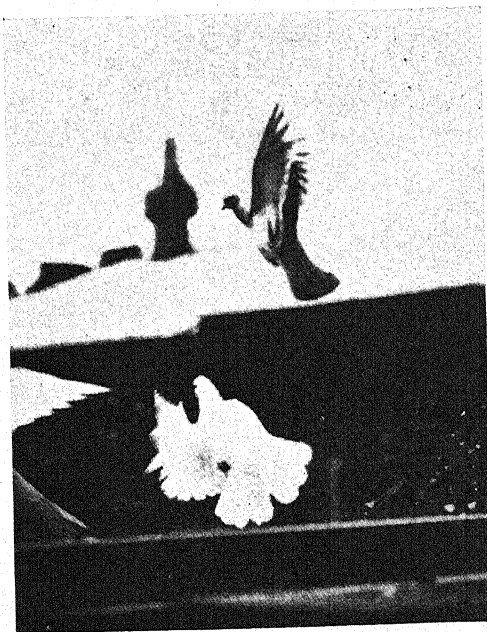


FIG. 6. PHASES OF THE WINGSTROKE

1) At the top of the upstroke, ready for the downstroke. (After Headley.)

the up-stroke the wing does not simply reverse the motion of the down-stroke. The angle of the wing is slightly altered

that a portion is hinged and movable approaches the solution of this problem. Warping of the wings would be preferable, however.

A description of soaring should begin with discussion of the air conditions necessary. Soaring appears never to have been observed in a dead calm. It usually occurs when there is a good breeze. It is frequently seen over rolling country and over waves. A choice spot for soaring seems to be above a sea cliff. Soaring occurs most frequently in semi-tropical countries which are subject to extreme variation in temperature. In such countries it may occur in the middle of the day even when there is only a slight

In the most usual form of soaring, the bird circles slowly. There is, however, considerable difference from one species to another with respect to soaring movements and the only generalization that can legitimately be made is that a soaring bird is never seen to maintain any given direction or speed for more than a moment at a time. While there are many pages devoted to the description of soaring birds few of them are as adequate as those of Hankin (7). His observations were made upon only a few species, chiefly vultures, kites and marabous, but they are of special value because they extended over a considerable period of time. The accurate observation of the flight of birds

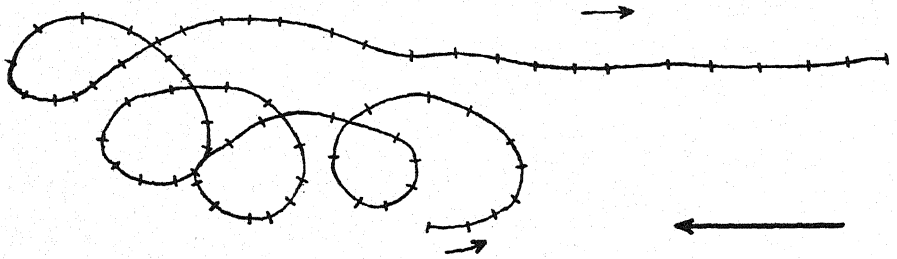


FIG. II. ONE OF HANKIN'S MIRROR TRACINGS OF A SOARING BIRD
The track is marked at one-second intervals. (After Hankin)

breeze and even over level country. It may occur at almost any altitude, although the range is limited by conditions to be noted below.

While soaring, a bird's wings are not held rigid, but are subject to constant slight alteration in angle and in flexion. There are movements of the wings at the shoulder and elbow and of the tail feathers, neck and head. The bird's speed and direction are constantly changing. There is continual shifting of the right-left and fore-aft angle at which it is tilted. Its altitude, too, constantly fluctuates. The rhythm of rise and fall is usually not periodic while that of turning in the horizontal plane is more often so.

at great heights requires training that comes only with such long study. In addition to direct observation of the birds by eye and binoculars, Hankin employed a mirror device which permitted him to make accurate tracings of the course of a bird (Figure II). Furthermore, a time marker was used so that later calculations could be made of the speed of the bird (in the horizontal plane) at any part of its course. Hankin wastes few words on theory, being satisfied to present as full a description of the facts as possible. It is regrettable that others have not extended his work to the many other soaring birds. A few of the important observations he has made will

be noted in a later paragraph, but the reader must be referred to the original for details.

Many of the theories of soaring which have been contributed are entirely inadequate. By no means all of them will be considered here. There is a theory which deserves attention only because its acceptance has caused some confusion. It is based upon the false assumption that just as a kite can rise in a strong wind, so can a bird. In the following discussion it should be clear that we are referring to a wind moving in the horizontal plane only, moving at a constant speed, and as a unit. A moment's consideration will indicate that a bird flying in such a body of air has no advantage over one flying in a perfect calm. In fact, a bird could not detect which of these two conditions held except by some reference (probably visual) to the earth beneath. The movement of the wind has in itself no lifting value except to an object which possesses and can maintain inertia antagonistic to such movement. A kite can stay up only so long as its string is intact. When this is cut it must fall (and would even if so balanced as to maintain an appropriate angle) for the difference in inertia it recently possessed is quickly overcome.

This theory has been applied by Ahlborn (according to Prochnow(21)), especially to birds which circle. Ahlborn maintains that when they move with the wind they acquire velocity with perhaps a slight loss in altitude, and that when they then wheel into the wind this velocity is converted into altitude. Certain of Hankin's observations appear to lend support to this view since they indicate that the speed of the bird is least on the windward side of the circle, followed by a sudden increase in speed as the bird goes down wind. The theorizers do not seem to have considered the fact that the gain

in altitude when the bird turns into the wind is made only at the cost of speed and with the result that, with each succeeding circle, there must be loss of distance to the leeward. Hankin and others have observed a bird circle for hours without such loss. If a bird could maintain altitude (without effort on its own part) by merely circling in a uniform wind it could maintain altitude by circling in a dead calm. This would be equivalent to perpetual motion.

Exner (5) (6) suggests that what appears to be soaring flight is really a modification of flapping flight. He supposes the wings to be moved with great rapidity and within very narrow limits. He offers little proof but calls attention to the rapid wing movements of insects and suggests that a somewhat similar humming sound can be heard emanating from soaring birds. The theory seems to have been adequately refuted (21) (24).

Besides these theories which appear to be quite inadequate there are three which are more acceptable. Each emphasizes a factor which doubtless operates in certain instances. We do not claim that any one of these factors alone or all taken together adequately accounts for all soaring although this may be the case. The present need is for more extensive and detailed records of soaring flight and of air conditions during such flight.

1. The theory of the direct variation of air velocity with altitude

To understand the merits of this theory one must bear in mind the conditions under which wind can be utilized by a bird to gain altitude. Wind in itself cannot be converted into lift except by a plane possessing inertia which is to some degree antagonistic to that of the wind. When a bird leaps from the ground against the wind it possesses this inertia, and the

wind striking the under surface of the wing is a lifting as well as a retarding force. If the wind be constant in speed at all levels its retarding influence will soon result in the loss of the bird's original inertia. The animal then will be borne along with the wind and all lifting force will cease. If, however, we were to assume that with each slight gain in altitude the bird encounters air which is moving more rapidly than that which it has just left we can see that the bird would

1000 feet at a height of seven and a half feet. Idrac's observations of the albatross (9) (10) indicate that the soaring of this bird is largely dependent upon velocity inequalities in the air immediately above the waves. The albatross constantly rises and falls above the water but it never attains any great altitude.

Many birds soar at heights of a thousand feet and more. It is improbable that at these heights the retarding influence of the earth upon the wind should result in sufficient velocity differences to account for soaring. This theory seems applicable only to flight within a few score feet of the earth's surface.

2. The theory of upward currents of air

The "bumps" encountered by aeroplanes furnish familiar evidence that there are air currents in other than the horizontal plane. There are three chief sources of such: the deflection of wind by irregularities in the earth's surface, the temperature changes resulting in rising and falling columns of air, and the deflection upwards of one air current by another.

Under certain conditions the upward movement of the wind is so pronounced that birds which cannot (or do not) ordinarily soar have been observed to perform maneuvers which might be described as such. Cliffs, hills, buildings, waves and ships may serve as deflectors (Figure 12). Birds which skim ocean waves no doubt are aided by such currents. Hankin notes that birds could soar over a tall fortress if there were a breeze, even when the air was otherwise (as will be noted below) unsoarable.

The significant relationship between temperature changes and the soaring of certain birds is emphasized by some of Hankin's observations. He classified birds with respect to their ability to

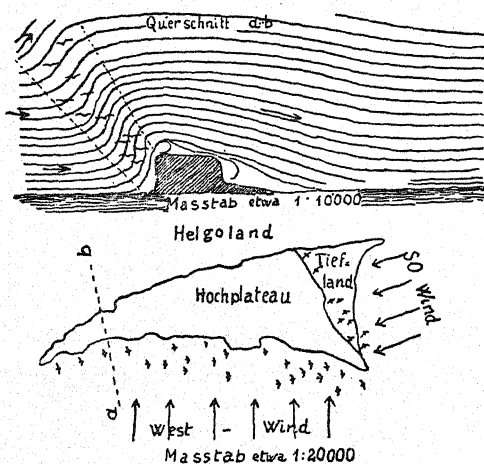


FIG. 12. DRAWING TO DEMONSTRATE RISING CURRENTS, CAPABLE OF SUPPORTING A SOARING BIRD, WHICH RESULT FROM DEFLECTION OF THE WIND BY A CLIFF OR HILLSIDE

(From Nimführ, R. 1919. *Mechanische und technische Grundlagen des Segelfluges*. Berlin. R. C. Schmidt.)

always possess inertia to some degree antagonistic to each succeeding level of air. This assumption may be justified for wind currents near the earth's surface because the friction of the earth must be considerable. Headley (8) has demonstrated this difference in speed at different levels, using an anemometer. On one occasion he recorded a velocity of 770 feet per minute at a height of two feet from the ground when the velocity was

soar (on the basis of their speed in gaining altitude, their structure, etc.) and observed that under some conditions no birds would soar, at other times only the best soarers would rise while under the most favorable conditions even the poorest were successful. Early in the morning none would rise. First the best soarers appeared and only later the heavier and less able birds. The birds ceased soaring in the late afternoon in the reverse order. It seems evident that with the heating of the earth by the sun, and thus of the air nearest the earth, a constant upward current was produced. Under the most favorable temperature conditions soaring was possible even though the wind velocity was very slight. At other times soaring required a good breeze.

In the third source of upward currents of air mentioned above, the deflection of one air current by another, we have a factor which is operative whenever there are appreciable air movements. When two gusts meet each other head on or at an angle there results deflection both upward and downward. The vertical movement is not so steady as that resulting from temperature changes or deflection by cliffs. Nevertheless, such thrusts may be strong while they last. The problem of the bird is to utilize all such vertical movements. The upward thrusts are capitalized to the fullest by appropriate wing expansion. The effect of the downward thrusts is minimized by alteration of the angle of the wings. The curvature of the wing surfaces is such as to aid in this process. The convex upper surface offers the minimum resistance to down-currents. The pressure on this surface is kept low since the air readily slips off the edges of the wing. The concave lower surface, on the contrary, cups the wind and wastes little of the available upward pressure.

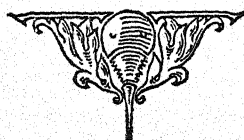
3. *A new theory*

The first two theories assist in the understanding of many instances of soaring. Nevertheless, there appear to be cases for which they alone cannot adequately account. How can a bird maintain its altitude in the absence of vertical air-currents (theory 2) and at heights too great for theory 1 to operate?

Insufficient attention has been given to the fact that most wind is gusty. Even a "steady" breeze is subject to constant fluctuation in speed and direction. In assuming such fluctuation it seems that we are not going beyond the facts. Given such fluctuation we are possessed with the basis of antagonistic inertia, that material which a soaring bird so efficiently converts into altitude. Let us assume that the bird is gliding into a wind. This air current suddenly eases and at the same time a current from a slightly different direction strikes its wings. The bird now possesses inertia antagonistic to this new gust and by wheeling can at once capitalize the difference in direction to the advantage of its altitude. The process continues indefinitely as the bird continually meets with irregularities in the air. Each such irregularity is the source of a stress which, theoretically, is capable of conversion into lift. Thus, there is constant readjustment to constantly shifting currents. Quite naturally a bird must, in the course of this procedure, adopt a circular or elliptical course if it is to remain soaring above a single section of the countryside, as any other course (excepting a much more involved course, such as a figure 8) would carry it away from its chosen position. Perhaps the greatest mystery of soaring is that which is usually taken for granted, the great sensitivity of the bird to shifting air-currents and the remarkable ability for rapid, coordinated and appropriate responses to these stimuli.

LIST OF LITERATURE

- (1) AIRY, H. 1883. Hovering of birds. *Nature*, London, 27: 294-5 and 336.
- (2) ———. 1883. Soaring of birds. *Nature*, London, 27: 590-2.
- (3) BEEBE, C. W. 1906. *The Bird. Its Form and Function*. New York, Holt, 496 p.
- (4) BILLARD, G. 1924. Les sacs aériens envisagés comme renforceurs du sens musculaire chez l'oiseau dans le vol et plus spécialement dans le vol à voile. *Ann. Sci. nat. Sér. zool.* 110, 7: 249-307.
- (5) EXNER, S. 1906. Ueber das "Schweben" der Raubvögel. *Pflügers Arch.*, 114: 109-42.
- (6) ———. 1907. Nochmals das "Schweben" der Raubvögel. *Pflügers Arch.*, 117: 564-77.
- (7) HANKIN, E. H. 1914. *Animal Flight. A Record of Observation*. London, Iliffe, 405 p.
- (8) HEADLEY, F. W. 1912. *The Flight of Birds*. London, Witherby, 163 p.
- (9) IDRAC, P. 1925. Experimental study of the "soaring" of albatrosses. *Nature*, London, 115: 532 (only).
- (10) ———. 1926. Le vol des albatross: observations et expériences au cours d'une mission d'étude dans les mers polaires du sud. *Rev. franc. Orn.*, 18: 38-46.
- (11) LANGLY, S. P. 1891. Experiments in aerodynamics. *Smithson. Contr. Knowl.*, 27: No. 1, 115 p.
- (12) ———. 1893. The internal work of the wind. *Smithson. Contr. Knowl.*, 27: No. 2, 23 p.
- (13) ———. 1911. Langly memoir on mechanical flight. (Edited by C. M. Manly. Two parts.) *Smithson. Contr. Knowl.*, 27: No. 3, 320 p.
- (14) LILIENTHAL, O. 1911. *Birdflight as the Basis of Aviation*. London, Longmans Green, 139 p.
- (15) LUCAS, F. A. 1916. The beginnings of flight. *Nat. Hist. New York*, 16: 4-11.
- (16) MAREY, E. J. 1890. *Le vol des oiseaux*. Paris, Masson, 394 p.
- (17) NEWTON, A. 1893-6. *Dictionary of Birds*. London, Adams & Black. 1088 p.
- (18) NOPSKA, F. 1907. Ideas on the origin of flight. *Proc. Zool. Soc. London*, 1907: 223-36.
- (19) ———. 1923. On the origin of flight in birds. *Proc. Zool. Soc. London*, 1923: 463-77.
- (20) OLSHAUSEN, A. 1908. Kritik der Exner'schen Theorie des Zitter- oder Schwirrfluges. *Pflügers Arch.*, 123: 433-53.
- (21) PROCHNOW, O. 1926. Die Verfahren zur Erforschung des Tierfluges. *Handb. biol. Arb. Meth.*, Abt. 9, Teil 4: 213-94.
- (22) PYCRAFT, W. P. 1922. *Birds in Flight*. London, Gay & Hancock, 133 p.
- (23) RAYLEIGH, LORD. 1899. The mechanical principles of flight. *Mem. Proc. Manchester Lit. Phil. Soc.*, 44: No. 5, 26 p.
- (24) SCHNEIDER, G. H. 1907. Bemerkungen zu Exner's Aufsatz: Ueber das Schweben der Raubvögel. *Pflügers Arch.*, 116: 283-98.
- (25) THOMSON, J. A. 1923. *The Biology of Birds*. London, Sidgwick & Jackson, 436 p.
- (26) TROWBRIDGE, C. C. 1906. Coasting flight. *Amer. J. Sci.*, 21: 245-69.





NEW BIOLOGICAL BOOKS

The aim of this department is to give the reader brief indications of the character, the content, and the value of new books in the various fields of biology. In addition there will frequently appear one longer critical review of a book of special significance. Authors and publishers of biological books should bear in mind that THE QUARTERLY REVIEW OF BIOLOGY can notice in this department only such books as come to the office of the editor. The absence of a book, therefore, from the following and subsequent lists only means that we have not received it. All material for notice in this department should be addressed to Dr. Raymond Pearl, Editor of THE QUARTERLY REVIEW OF BIOLOGY, 1901 East Madison Street, Baltimore, Maryland, U. S. A.

BRIEF NOTICES

EVOLUTION

THE NEW EVOLUTION. ZOÖGENESIS.

By Austin H. Clark.

The Williams and Wilkins Co.

\$3.00 5 $\frac{5}{8}$ x 8 $\frac{1}{2}$; xiv + 297 Baltimore

In this book Dr. Clark presents a graphic picture of the plasticity of the organism and the closeness and complexity of its relation with the environment. No recent work on evolution has stirred up such impassioned controversy as has this book. It has, indeed, risen to the heights of calling Dr. Clark bad names. The gist of his evolutionary doctrine is summed up in the following passage:

In tracing the history of animal life from its very first appearance to the infinite complexity which we see at the present day there are three entirely separate sets of facts to be considered, and any acceptable theory of the development of animal life must harmonize and correlate all three.

In the first place, within each of the so-called phyla or major groups of animals, as is well seen in the vertebrates, particularly in the mammals and the reptiles, there are many well marked, obvious, and undeniable evolutionary lines which, beginning with a relatively simple form of creature run by easy stages to a specialized and highly complex form.

In the second place, very few of these evolutionary lines are perfectly continuous. Practically all of

them are more or less interrupted by gaps of various widths, and these gaps are often very broad. Especially is it true that these evolutionary lines tend to be separated from each other for their entire course, running parallel or more or less convergent right down to their very earliest beginnings, and not uniting in a common type of animal as we would expect. For instance, the whales and the seals are always whales and seals, and show little or no approach to any other type of mammal. Similarly, there are no intermediates between turtles and snakes, or between turtles and lizards, all of which are reptiles, or between squid and oysters, though both types are mollusks.

In the third place, no animals are known even from the very earliest rocks which cannot be at once assigned to their proper phylum or major group on the basis of the definition of that group as drawn up from a study of living animals alone. A backboneed animal is always unmistakably a backboneed animal, a starfish is always a starfish, and an insect is always an insect no matter whether we find it as a fossil or catch it alive at the present day. There can be only one interpretation of this entire lack of any intermediates between the major groups of animals, as for instance between the vertebrates, the echinoderms, the mollusks and the arthropods. If we are willing to accept the facts at their face value, which would seem to be the only thing to do, we must believe that there never were such intermediates, or in other words that these major groups from the very first bore the same relation to each other that they do at the present day. Is this creationism? Not at all. It simply means that life at its very first beginnings from the single cell developed simultaneously and at once in every possible direction. All of the phyla

or major groups seem to be of simultaneous development—at least we have no evidence that it was otherwise. From each one of these a separate developmental line or tree arose, growing upward through the ages.



THE PROGRESS OF LIFE. *A Study in Psychogenetic Evolution.*

By Alexander Meek.

Longmans, Green and Co.

\$4.20 $5\frac{1}{2} \times 8\frac{1}{2}$; vii + 193 New York

The opening sentences of the preface of this book read:

This work is not meant to introduce a new theory but to indicate a way to recover that elasticity of conception of the processes of evolution which the behaviour of protoplasm invites and which the germ-plasm theory of development has for so many years prevented. The inadequacy of the theory has become more and more apparent and in my opinion the time for its recession has been long overdue.

So far as we have been able to determine, the author has stated little that is new, and a good deal that seems questionable. Exactly what his position is we have not discovered; he appears, however, to be a follower of Butler and Semon. He emphasizes at length the fact that the environment plays an important part in determining the characteristics of the individual. The briefest statement of his views is given at the end of Chapter V:

The free cell and the germ cell, each of them, can do nothing else but give rise by growth to the kind of cell or the kind of soma from which it has arisen, and it needs to accomplish the history an environment which supplies the food and the energy.

We cannot avoid the suspicion that the somewhat confused language in which the book is written may derive in some measure from a lack of clarity in the ideas of the writer.



THE GENETICAL THEORY OF NATURAL SELECTION.

By R. A. Fisher. *Oxford University Press*
\$6.00 $6\frac{1}{4} \times 9\frac{1}{4}$; xiv + 272 New York

This book falls into two sharply contrasted parts, in the first of which Dr. Fisher speaks with the accent of the physical biologist, but in the second with that of the eugenicist. The direction of evolution, he concludes, is determined, not by the direction of mutation but by that of selection. To the reviewer this conclusion seems in some part paradoxical. Can any selective process, however stringent, succeed in drawing a population of green balls from an urn containing only black balls? And, if some of the black balls mutate to red, does the resulting increase in variance in any way aid selection in its task of picking out the green balls that are not there? Of course, if black balls mutate to both red and green but more frequently to red, selection may pick out the rare green mutations rather than the more common red ones, but in this case both mutation and selection have their effect on the direction of evolution.



THE KEY TO EVOLUTION. *In Four Double Volumes. Vol. 1, How Life Began. Vol. 2, How Plants Arose. Vol. 3, The Origin of Animals. Vol. 4, The Origin of the Backboned Animals. Vol. 5, From Amphibian to Man. Vol. 6, Man, Cousin to the Apes. Vol. 7, Embryology and Evolution. Vol. 8, Causes and Methods of Evolution.*

By Maynard Shipley. *Haldeman-Julius Co.*
Girard, Kansas

\$2.45 for set of four double volumes

$5\frac{1}{2} \times 8\frac{1}{2}$; 64 pages each (paper)

Why is Haldeman-Julius permitted to stay in business in Kansas? This problem has long troubled us. Have the Ku Kluxers no pride, that they have not tarred and feathered him long since? Anyhow, they have not, and he continues

to publish incendiary and blasphemous stuff, and, presumably, to sell it in quantity. The present work is an unusually ambitious one. It attempts to tell the whole story of evolution, from the Galaxy to *Homo sapiens*, with full documentation, and frequent beltings of the Fundamentalists and Henry Fairfield Osborn. It is, incidentally, quite well done.



STUDIES ON THE EVOLUTION OF THE PELVIS OF MAN AND OTHER PRIMATES. *Bulletin of The American Museum of Natural History, Vol. LVIII, Art. XII.*

By Harriet C. Waterman.

American Museum of Natural History
65 cents $6\frac{1}{4} \times 9\frac{1}{2}$; 58 (paper) New York

The author bases her study upon the form of the pelvis of man and other primates and the function of the muscles involved. In the summary there is given a list of the "habitus and heritage characters in the ilium and ischium of the animals studied," also a list of "the habitus and heritage characters in the musculature of the main groups." Her conclusions support Gregory's (1920) views as to the main stages in the evolution of the pelvis from the primitive arboreal quadrupeds to man. The report includes tables of measurements of bones and muscle fibers of the forms under consideration and figures of pelvic and femoral bones and their musculature. There is a bibliography of 32 titles.



GENETICS

EINFÜHRUNG IN DIE VERERBUNGS-LEHRE.

By Erwin Baur. *Gebrüder Borntraeger*
21.50 marks $6\frac{3}{8} \times 10$; vii + 478 Berlin

A revision of this excellent introduction

to the study of inheritance which is by way of becoming a classic textbook. Rather more attention is given to the botanical side than most texts allot, and there is perhaps less tendency to assume that *Drosophila* suffices to explain all heredity in every organism. The book is profusely illustrated, has a good index, and an excellent list of literature for the student.



GENETICS. *An Introduction to the Study of Heredity.*

By Herbert E. Walter. *The Macmillan Co.*
\$2.50 $4\frac{7}{8} \times 7\frac{1}{4}$; xxi + 359 New York

The author has completely overhauled this book, and brought it well up to date. It is a thoroughly sound textbook written in the author's usual delightful style. No college student of zoology should fail to read it.



DAS DETERMINATIONSPROBLEM IN ANALYTISCHER DARSTELLUNG.

By Adolf Cohen-Kysper. *Julius Springer*
4.80 marks $6\frac{1}{2} \times 9\frac{1}{2}$; 48 (paper) Berlin

A discussion of the factors underlying ontogenesis, which emphasizes that the genes are not independent factors, each producing its effect on development in isolation from the others, but that the organism as a whole is a system, the parts of which are in their turn systems of lower order, and so on. The author warns that the results obtained in experiments on regulation may lead to misinterpretations when applied to questions of normal development.



LES GROUPE SANGUINS. *Schémas et Applications Pratiques.* LA TRANSFUSION SANGUINE. *Technique et Indications.*

By Paul Michon. *Masson et Cie*
16 francs $5\frac{1}{2} \times 7\frac{7}{8}$; 120 (paper) Paris

A brief account of blood-groups, and of the technique of blood transfusion.



MENDEL'S PRINCIPLES OF HEREDITY, *Fourth Impression.*

By W. Bateson. *The Macmillan Co.*
\$5.00 6 x 9; xiv + 413 New York



GENERAL BIOLOGY

THE USE OF THE MICROSCOPE. *A Handbook for Routine and Research Work.*
By John Belling. *McGraw-Hill Book Co., Inc.*
\$4.00 5 $\frac{3}{4}$ x 9; xi + 315 New York

This book contains much valuable information, badly presented, for the practising worker with the microscope who has a reasonable familiarity with the theory of his instrument. It is not a book that will be of much service to the beginner. To take one example: We find on page 19 the statement "There can be no understanding of the microscope without understanding aperture;" but we defy anyone to arrive at an understanding of aperture on the basis of what is to be found in this book. There is an index, not too good, and a bibliography of 157 titles.



ÜBER DEN UNTERSCHIED VON MINERALIEN UND LEBEWESSEN. *Öffentlicher Vortrag, gehalten am 18. Dezember 1929 in Berlin.*

By Arrien Johnsen.

Gebrüder Borntraeger

4.50 marks 5 $\frac{1}{2}$ x 8 $\frac{1}{2}$; 41 (paper) Berlin

We have already been instructed by an eminent physicist on "How to Tell the Birds from the Wild Flowers." In this interesting lecture an eminent mineralogist considers some of the likenesses and

differences between minerals and living beings. Crystals, like living beings, undergo growth, regeneration, natural selection, and mutation. Heterogeneity is, however, a necessary, though not a sufficient condition of living substance. In this respect amorphous minerals stand nearer to living beings than do crystals.



FIELD BOOK OF PONDS AND STREAMS. *An Introduction to the Life of Fresh Water.*

By Ann H. Morgan. *G. P. Putnam's Sons*
\$3.50 3 $\frac{3}{4}$ x 6 $\frac{3}{4}$; xvi + 448 New York

Dr. Morgan, Professor of Zoology of Mount Holyoke College, is by her training as a teacher and a collector well fitted for the task which she has set herself. Not only has she produced a thoroughly dependable guide but a fascinating one. The numerous illustrations in color, half-tones and black and white drawings, have been fittingly chosen. The keys make identification of the different species a simple matter. There is a lengthy bibliography, a glossary and an excellent index.



LA SOLUTION DU MYSTÈRE DE LA MORT.

By J. L. W. P. Matla. *Gaston Doin et Cie*
65 francs (paper) Paris
75 francs (cloth)

6 $\frac{1}{4}$ x 9 $\frac{1}{2}$; vi + 284 + 6 plates

A description of experiments to determine the volume of the soul, which, the author concludes, is material and therefore not immortal, but continues to exist for a limited time after the death of the body. It is not altogether surprising that his conclusion has failed to commend itself to either physicists, spiritists, or the orthodox religious.

THE SCIENCE OF BIOLOGY. *An Introductory Study. Revised Edition.*

By George G. Scott. Thomas Y. Crowell Co.
\$3.75 $5\frac{5}{8} \times 8\frac{3}{8}$; xx + 633 New York

The revised edition of this excellent text retains the plan by which the different plant and animal phyla are studied before considering general biological problems. The book is clearly written and covers a wide range of topics.



BIODYNAMIQUE GÉNÉRALE. *Fondée sur l'Étude du Tourbillon Vital d'Éther.*

By Alfred Lartigue. Gaston Doin et Cie
20 francs Paris

$5\frac{5}{8} \times 9\frac{1}{8}$; iv + 156 (paper)

M. Lartigue wishes to base the structure and functions of living beings on vortices in the ether. The argument suffers from the defect common to arguments from *simulacra vitae*: the likeness of two patterns does not necessarily prove the likeness of the causes producing them.



DICTIONARY OF BIOLOGICAL EQUIVALENTS. *German-English.*

By Ernst Artschwager.

The Williams and Wilkins Co.

\$4.50 6 x 9; 239 Baltimore

A useful book for the student of biology. The author has succeeded in being a far more complete and thorough lexicographical help to the biologist than have any previous dictionaries. The English meanings for the German words are well chosen.



FOUNDATIONS OF BIOLOGY. *Fourth Edition.*

By Lorande L. Woodruff. The Macmillan Co.
\$3.50 $5\frac{1}{2} \times 8\frac{1}{2}$; xvi + 501 New York

MANUAL OF BIOLOGY.

By George A. Baitsell. The Macmillan Co.
\$2.60 $5\frac{1}{2} \times 8\frac{1}{2}$; xiv + 369 New York

New editions of these well known texts, which have been worked out for use together.



EINFÜHRUNG IN DIE BODENKUNDE DER SEEN. *Die Binnengewässer. Band IX. By Einar Naumann.*

E. Schweizerbart'sche Verlagsbuchhandlung
16 marks (paper) Stuttgart
17.50 marks (cloth)

$6\frac{3}{4} \times 10$; ix + 126



A TEXT-BOOK OF BIOLOGY. *For Students in General, Medical and Technical Courses; Sixth Edition, Thoroughly Revised.*

By William M. Smallwood. Lea and Febiger
\$4.00 net $5\frac{3}{4} \times 9\frac{1}{8}$; 470 Philadelphia



LABORATORY MANUAL OF GENERAL BIOLOGY

By George G. Scott. Thomas Y. Crowell Co
\$1.00 $5\frac{1}{2} \times 8\frac{5}{8}$; xi + 125 New York



LABORATORY STUDIES, DEMONSTRATIONS, AND PROBLEMS IN BIOLOGY.

By Nathan H. Kingsley and Edward J. Menge. Bruce Publishing Co.

\$1.28 $8\frac{1}{2} \times 11$; 208 (paper) Milwaukee



HUMAN BIOLOGY

ROCK PAINTINGS OF SOUTHERN ANDALUSIA. *A Description of a Neolithic and Copper Age Art Group.*

By Abbé Henri Breuil and M. C. Burkitt, with the collaboration of Sir Montagu Pollock.
Oxford University Press

\$25.00 New York
10 x 12 $\frac{1}{2}$; xii + 88 + 33 plates and 7 maps

An account, with many excellent plates, of the neolithic and copper age paintings in the rock shelters of southern Spain.

It is an important as well as a very interesting book. The bulk of the work upon which this book is based is due to M. Breuil. Sir Montagu Pollock translated the condensed notes, and contributed a good deal on nomenclature. Mr. Burkitt contributed the Introduction and Conclusion, as well as some of the photographs.

There are generally recognized now three "groups" of prehistoric Spanish art. The first of these art groups is typified by the paleolithic cave paintings, of which the best example is the wonderful frescoed ceiling of Altamira. Some of our readers will perhaps be surprised to learn that Mr. Burkitt, in this book, dates these paintings with the following statement: "The visitor . . . can only rest amazed at the artistic ability of these early folk who lived perhaps ten thousand years and more ago." We should have thought a good deal more.

Art Group II is the earliest rock shelter art of eastern Spain. This art Burkitt believes to be not far in date from the cave art of Art Group I, though so different from it as to indicate that entirely different tribes of people were involved in its doing. It is characterized in two ways: first, the animals differ from the Group I animals in the same sort of way that the animals of a good Japanese artist differ from those of Rosa Bonheur; second, human figures are frequent, whereas they occur only rarely in cave art.

Art Group III is another, and presumably much later, rock shelter art, which has its center and focus in Andalusia, though much of it is found in the provinces of southern Spain further to the east. It is with this Art Group III that the present book is concerned. It is characterized primarily by its completely conventionalized patterns, or symbols.

These paintings are often found superposed upon paleolithic Group II drawings on the same rock walls.

The authors are extremely cautious and conservative in the matter of conclusions. As to dating they make at least a plausible, if not quite conclusive case, that the painters were of a neolithic and perhaps copper age culture. As to the motive and meaning of the paintings no conclusion is reached. Various possibilities (religious, marriage, talismanic protection, etc.) are suggested, but they carry no conviction.

The book must be regarded as a splendid objective record of an extremely interesting lot of artefacts made by prehistoric man. The interpretation of this record must wait upon further research.



CAUSES OF DEATH BY OCCUPATION.

Occupational Mortality Experience of the Metropolitan Life Insurance Company, Industrial Department 1922-1924. Bulletin of the United States Bureau of Labor Statistics No. 507.

By Louis I. Dublin and Robert J. Vane, Jr.

*U. S. Government Printing Office
Washington*

25 cents

5 $\frac{3}{4}$ x 9 $\frac{1}{8}$; iv + 130 (paper)

This study is based upon a group of industrial policy holders (105,467 white males) of the Metropolitan Life Insurance Company, whose occupations were in manufacturing plants, mines, transportation, industries and mechanical plants. The statistics deal with occupied individuals who died during the years 1911-13 and 1922-24. Space will permit only a few of the interesting results which the analysis of this data shows. It is found that

within the same social class the death rates of male wage earners are uniformly higher than those of females. Their death rates also exceed those prevail-

ing among males in the general population and among males insured under ordinary policies in the same company. Differential death rates of various age groups show that this disparity increases year by year up to about age 54. Compared with workers in nonhazardous employments, wage earners are at a disadvantage in respect to every important cause of death. The death rate from tuberculosis, age for age considered, is especially high in the industrial group and ranges from two and a half to nearly four times that of the nonindustrial population. Deaths from pneumonia and accidents are over twice as frequent; while death rates from the degenerative diseases are from two to three times as great.

There are 78 tables in the text and a list of 26 references is given.



HANDS AND FACES. *The Book of Temperaments. Being the Third and Concluding Volume of "The Book of the Hand."*

By Katherine St. Hill.

Rider and Co.

10 shillings 6 pence net

London

6 x 9; 160

In this book the author turns from palmistry to physiognomy, illustrating her types with the portraits of historical personages. "I should very much have liked to adorn my pages and portray my characters with examples of living personages of great importance, but I have been advised by the wise and learned that if amid my studies the cap which fitted was not of the most laudatory I should be in danger of actions for libel, and on the axiom that 'the greater the truth the greater the libel' I could be seriously punished."

The book cannot be taken as a serious contribution to the interesting but difficult subject of constitutional types; the author has, however, a sharp pen and such bits as the following will repay the casual reader:

Venus-Luna is very ineffective and helpless. These subjects always want to be worked for and taken care of. "They want to go to Heaven in a hand-

basket," as an old Devon woman said of one of them. Whatever they have in the world they cannot hold on to, and are soon robbed of it by some clever Mercurian or greedy Saturnian person. But if properly guarded and cared for they are gentle and grateful, and never rebel against coercion. They love quiet and comfort, and will employ themselves in all sorts of little kind actions, and are often very restful if not very intelligent companions to the more strenuous temperaments. They go into the Church, and are good curates, considerate, pious, and sympathetic. The women take to writing verse and visiting cottages.



**GRUNDZÜGE DER VERERBUNGS-
LEHRE, RASSENHYGIENE UND BE-
VÖLKERUNGSPOLITIK für Gebildete aller
Berufe.**

By Hermann W. Siemens.

J. F. Lehmanns Verlag

München

3 marks (paper)

4 marks (cloth)

$4\frac{7}{8} \times 7\frac{1}{2}$; 147

The fourth edition of this popular tract on heredity and eugenics, which has been translated into Swedish, English, and French (a Dutch translation is announced). As this type of uplift goes, the book is well done. Some of the data introduced, however, rather give us pause. For example, we find the following table showing the relation between the price of hats and the sizes available at these prices:

Price of Hat marks	Largest available size	Mean size
3	56	54
6	57	55
7	59	56
12	60	57
24	61	58

The argument then runs: high-priced hats are larger. Therefore the people who buy them have bigger heads; but brain size is correlated with head size, and mental endowment with brain size; hence the rich are better endowed mentally than the poor.

A HISTORY OF THE JEWS.

By Abram Leon Sachar.

Alfred A. Knopf, Inc.

\$5.00 $6\frac{1}{4} \times 9\frac{1}{4}$; xli + 408 New York

To write a history of the Jews is an ambitious undertaking and to compress it into one volume is indeed a difficult task. One cannot but feel upon laying down this book that the author still has much to say. Nevertheless he has contributed a highly interesting and authentic account covering thirty centuries of Judaism. Throughout the book, whether in discussing the golden age of the Jews in Moslem Spain, the ghetto, Jewish mysticism, the influence of the French Revolution upon the Jews, the Russian pogroms, or the Jew in the new industrial world, the author has maintained a singularly objective viewpoint. Of especial interest to readers of these pages will be the sections dealing with the history of the Jews in America. The work includes eight maps in color, a bibliography and an index.

ÉTAT SOCIAL DES PEUPLES SAUVAGES. *Chasseurs. Pêcheurs. Cueilleurs.*

By Paul Descamps.

Payot

30 francs $5\frac{1}{2} \times 9$; 288 (paper) Paris

This book treats the social organization of peoples who are still in the hunting or fishing stage, and especially the influence of their modes of hunting or fishing on other social categories, such as the matriarchate or totemism. M. Descamps finds himself unable to agree with those facile generalizers, the Optimists, that the story of human evolution is a record of universal progress, physical, technical, moral, and intellectual, nor, on the other hand, with the Pessimists that as the arts advance, morals decay. Social evolution, he concludes, is to be figured, not as a linear series, but as a tree with diverging branches. Not all peoples have

passed through a totemic phase, nor a boomerang stage, nor a period of cannibalism. The development of each people must be worked out *ad hoc*.



THE DIAGNOSIS OF HEALTH.

By William R. P. Emerson.

D. Appleton and Co.

\$3.00 $5\frac{1}{4} \times 8$; xiv + 272 New York

This is an interesting and rather annoying book. It is interesting in that it shows at considerable length that a large amount of ill-health, especially in young people, can be remedied by relatively simple measures. It is irritating because one cannot avoid the feeling that health is being judged by an arbitrary yard-stick (weight for height) which makes inadequate allowance for individual variation. We do not accuse Doctor Emerson of this; doubtless in the cases which he handles, individual peculiarities are fully taken account of. But we strongly suspect that when the system is adopted, the school authorities will insist that any child who is under "normal" weight for height is under-nourished, regardless of what other skeletal measurements may show.

MAORI WITCHERY. *Native Life in New Zealand.*

By C. R. Browne. J. M. Dent and Sons, Ltd.

\$2.00 $5\frac{1}{8} \times 7\frac{1}{4}$; x + 210 London and Toronto

Somewhat in the style of fiction, Mr. Browne, who was a government railway surveyor, gives a most interesting account of the domestic manners and customs of the Maoris of New Zealand, as they existed a third of a century and more ago. The book is mainly autobiographical, the author having himself married a Maori girl. The account of the manner in which the witch doctor brought about her death is one of the principal incidents

of the book. One gathers the impression from the book that the Maoris were a fine pagan race before their contact with whites. Their chief intellectual interest appears to have been in *risqué* jokes and stories.



THE BIOLOGICAL BASIS OF HUMAN NATURE.

By H. S. Jennings.

W. W. Norton and Co., Inc.

\$4.00 $5\frac{3}{4} \times 8\frac{1}{2}$; xviii + 384 New York

This book is written primarily for the general reader, and has had a great popular success. We liked particularly the chapter on Biological Fallacies and Human Affairs, in which Professor Jennings displays and dissects some of the fallacies which abound in eugenic and other uplift, and which are not altogether unheard of in strictly scientific literature. His discussion of eugenics is fair and sane; we fear that it will hardly be extensively quoted for propaganda purposes by either side. The final chapter, on emergent evolution, left us rather cold. We should have felt better, perhaps, if he had not used as an argument against mechanism that its moral effects are bad. This sounds too much like what we have heard so often from the pulpit.



CHILDREN IN FRUIT AND VEGETABLE CANNERIES. *A Survey in Seven States.* United States Department of Labor, Children's Bureau, Publication No. 198. By Ellen N. Matthews.

U. S. Government Printing Office

40 cents

Washington

$5\frac{3}{4} \times 9\frac{1}{8}$; vii + 227 (paper)

A survey of child labor in canneries in Delaware, Indiana, Maryland, Michigan, New York, Washington, and Wisconsin. Canning is a highly seasonal industry, employing a high percentage (over one-

half) of women, and a considerable number of children. Especially in the eastern states a good deal of migratory labor is employed. Maryland and Delaware show the highest proportion of children under fourteen; they also show the highest percentage of children working a maximum of ten hours or more daily. It appears from the survey that compliance with the child labor laws depends on the energy of the officials charged with enforcement.



CHILD LABOR. *Facts and Figures.* United States Department of Labor. Children's Bureau. Bureau Publication No. 197. U. S. Government Printing Office

25 cents

Washington

$5\frac{3}{4} \times 9\frac{1}{8}$; viii + 133 (paper)

This is the third in a series of publications concerned with the analysis of information on the various aspects of child labor. The material, some of which has been previously published, is arranged under five headings, as follows: A history of the movement for the prohibition and regulation of child labor; extent and distribution of child labor in the United States; the causes, social cost, and prevention of child labor; the present legal status of child labor in the United States; vocational guidance and vocational education. A list of reading references is given.



THE ART AND RELIGION OF FOSSIL MAN. *Translated by J. Townsend Russell, Jr.*

By G.-H. Luquet. Yale University Press

\$5.00 $6\frac{1}{4} \times 10$; xiv + 213 New Haven

A short but good and well-illustrated account of Paleolithic art and religion. The chapters on art are much better than those on religion, as is natural; our views on the religion of Paleolithic man are, and

seem likely to remain, very largely based on inference, hypothesis, analogy, and prejudice.

The present author is, as anthropologists go, a cautious man; he rejects a vast deal of cheerful guess-work reasoning about his subject; but a good deal is left which seems to us to go a long way beyond what the facts warrant.



TIZOC, GREAT LORD OF THE AZTECS, 1481-1486. *Contribution from the Museum of the American Indian, Heye Foundation, Vol. VII, No. 4.*

By Marshall H. Saville.

Museum of the American Indian, Heye Foundation

\$1.60 $6\frac{3}{4} \times 10$; 78 (paper) New York

The author incorporates in this study extracts from the writings of ancient chroniclers and of later students of Aztec history together with a detailed study of the sculptures of the Stone of Tizoc, a very fine golden statuette of this seventh great lord of the Aztecs, and the inscriptions on a tablet of obsidian relating to this period. The work contains many illustrations, numerous notes relating to the text and a list of works consulted. There is no index.



NIEDERSÄCHSISCHE BAUERN. I. *Geestbauern im Elb-Weser-Mündungsgebiet (Börde Lamsstedt).*

By Wilhelm Klenck and Walter Scheidt.

Gustav Fischer

8 marks (paper)

9.50 marks (cloth)

$6\frac{3}{4} \times 10\frac{1}{2}$; ix + 112 + 8 tables

This intensive study of the peasants of a small district between the estuaries of the Elbe and the Weser is, it is hoped, the first of a series of monographs on the *Rassenkunde* of the German people. After a preliminary sketch of the geography

and history of the region, the economic and cultural organization and the physical anthropology of the inhabitants are treated.



VARIATIONS IN DEVELOPMENT AND MOTOR CONTROL IN GOITEROUS AND NON-GOITEROUS ADOLESCENT GIRLS.

By Louise A. Nelson.

Warwick and York, Inc.

\$2.75 + 10¢ postage

Baltimore

$5\frac{1}{8} \times 7\frac{5}{8}$; xii + 193

Dr. Nelson finds no significant difference between goiterous and non-goiterous girls in ability to inhibit movement or to coordinate eye and hand movements. She concludes that degree of enlargement of the thyroid gland is not a satisfactory measure of its functional activity.



THE U. S. LOOKS AT ITS CHURCHES.

By C. Luther Fry.

Institute of Social and Religious Research

\$2.50 6×9 ; xiv + 183 New York

An examination of the 1926 Census of Religious Bodies. In addition to discussion of the published data, there is an interesting section on the educational qualifications of ministers, based on material collected but not published by the Census Bureau.



JUVENILE DELINQUENCY IN MAINE.

United States Department of Labor. Children's Bureau Publication No. 201.

U. S. Government Printing Office

15 cents $5\frac{3}{4} \times 9$; v + 90 Washington

The report of a survey made at the request of the Maine Department of Public Welfare. It consists chiefly of case reports, with a final section of recommendations for getting rid of some more of the taxpayer's money.

DRAMAS OF FRENCH CRIME. *Being the Exploits of the Celebrated Detective*

René Cassellari. Hutchinson and Co., Ltd.
18 shillings net 6 x 9; 288 London

Mildly entertaining stories of the work of the Sûreté Générale. On the whole we prefer to stick to fiction; Sherlock Holmes seems to us a more interesting detective than M. René Cassellari.



THE ANATOMY OF MUSIC. *A Complete Popular Outline of Musical Theory.*

By Winthrop Parkhurst.

Alfred A. Knopf, Inc.

\$2.50 5½ x 7½; xix + 200 New York

This book is intended to give the music lover who has been content with passive listening enough knowledge of the principles of the subject that, hearing, he may understand.



ZOOLOGY

THE OLIGOCHAETA.

By J. Stephenson.

Oxford University Press

\$20.00 6¼ x 9¾; xvi + 978 New York

This comprehensive survey of the Oligochaeta will long serve as a source book for zoologists, physiologists and experimentalists. About one fourth of the volume is devoted to classification and bibliography. In the remaining pages the author has gathered together, with much care and discrimination, material which has appeared on the biology of the Oligochaetes within the last 34 years. For earlier results the reader is referred to the monographs of Vejdovsky and Beddard. In the present work not only are the anatomy, histology, embryology and reproduction of these animals discussed but there are included chapters on anomalies of structure, regeneration, ecology

and manner of life, geographical distribution, as well as minor subjects. There is even a section on the Oligochaetes in commerce, as food and as medicine. In fact, practically all that is known of the Oligochaetes is to be found within these pages. The author deserves much praise for the arrangement and presentation of the material. His simple and entertaining style makes this part of the book interesting reading even to the layman.

No attempt has been made to deal in a comprehensive manner with the systematic section, the survey stopping at the genera. Likewise in the bibliography of over 1000 items, only systematic papers which furnish data for the general chapters are as a rule included. The book contains many illustrations, also subject and systematic indices. It is a model of monographic writing.



WILD ANIMALS IN AND OUT OF THE ZOO.

By William M. Mann.

Smithsonian Institution Series, Inc.

6¼ x 9½; 362 New York

This beautifully printed and illustrated volume, by the distinguished Director of the National Zoological Park, is a valuable contribution to the literature relating to zoological gardens, and there are few subjects more fascinating. It forms the sixth volume of the Smithsonian Scientific Series. Unfortunately, as it seems to us, it cannot be separately purchased. The series, which is a private commercial publishing enterprise, must be subscribed to as a whole, and at a price (\$198 for the twelve volumes bound in vellum, \$150 bound in buckram) which is doubtless not high relatively, considering the quality of the product, but is absolutely great enough to keep the set off the shelves of most working scientific men, in all probability.

Dr. Mann's book is full of entertaining zoo lore, collecting experiences, notes on habits, etc. The history of the National Zoological Park is reviewed, and tables are given in the appendices, showing first the numbers, species, and maximum longevity (in captivity) of all the animals that have ever lived in that zoo; and second, the numbers and species of animals born there. A notable book.



STUDIES OF COMMON FISHES OF THE MISSISSIPPI RIVER AT KEOKUK.

Bureau of Fisheries Document No. 1072.

By Robert E. Coker.

U. S. Government Printing Office
50 cents $7\frac{1}{2} \times 11$; 85 (paper) *Washington*

This survey is restricted largely to those species of fishes of which 50 or more individuals were observed. Special attention is given to their economic importance, breeding habits and range, known or supposed migration, seasonal occurrence and their abundance both before and after the construction of a great dam for hydroelectric power between Keokuk, Iowa, and Hamilton, Illinois. During the course of the survey many problems of considerable significance appeared concerning fishes of the Mississippi River and the author discusses a group of these problems in the concluding pages of his paper. The work contains illustrations of many of the fishes under discussion, charts and tables and a lengthy bibliography. There is no index.



THE LIFE AND LETTERS OF SIR HARRY JOHNSTON.

By Alex. Johnston.

Jonathan Cape and Harrison Smith
\$3.50 $5\frac{1}{4} \times 8$; 351 *New York*

Sir Harry Johnston's chief contribution to zoology is his discovery of the Okapi, but throughout his travels and explora-

tions in Africa he was constantly recording his observations and discoveries either with brush or with pen. In these pages we have a highly interesting, if somewhat eulogistic, account of the achievements of this versatile man as scientist, artist and explorer and as fighter, Governor and history maker of Africa.



ANIMAL LIFE OF YELLOWSTONE NATIONAL PARK.

By Vernon Bailey.

Charles C. Thomas.

\$4.00 postpaid

Springfield, Ill.

6 x $8\frac{3}{4}$; xiii + 241

This is an entertaining book for the layman or the amateur, who intends to visit our most popular national park, to include in his kit-bag. It is devoted chiefly to mammals and birds. Written by a trained naturalist of wide experience, it is accurate. With the exception of the scientific name of each animal which is always given with the common name, the book is devoid of technical terms or descriptions. There are numerous illustrations, a map of the park and an index.



THE FAUNA OF BRITISH INDIA, INCLUDING CEYLON AND BURMA. *Cestoda, Vol. I.*

By T. Southwell.

Taylor and Francis

22 shillings 6 pence

London

6 x 9; xxxi + 391

In this volume the author has sought to bring together all the information at present obtainable regarding the cestodes of India. He states, however, that the field is largely unexplored. The work is well illustrated and has a lengthy list of references. There are systematic and alphabetical indices.



DIPTERA OF PATAGONIA AND SOUTH CHILE. *Based Mainly on Material*

*in the British Museum (Natural History).
Part I—Crane-Flies.*

By C. P. Alexander.

British Museum (Natural History)
15 shillings London

$5\frac{1}{2} \times 8\frac{1}{2}$; xvi + 240 + 12 plates

This monograph is based largely on the collection made by Edwards and Shannon in 1926. The author concludes, from the resemblances to the Australasian fauna, that "the evidence seems overwhelmingly in favour of a former Antarctic land connection."

PRAKTIKUM DER ZÜCHTUNG VON
WARMBLÜTERGEWEBE IN VITRO.

By Fritz Demuth.

Rudolph Müller und Steinicke
6 marks (paper) München

7.20 marks (bound)

$5\frac{5}{8} \times 8\frac{1}{8}$; 116

A *vade mecum* for tissue culture workers.

A TEXT-BOOK OF ECONOMIC ZO-
OLOGY.

By Z. P. Metcalf.

\$4.00 net

Lea and Febiger

Philadelphia

$5\frac{3}{4} \times 9\frac{1}{8}$; 392

LABORATORY STUDIES IN ZOOLOGY

By H. D. Reed and B. P. Young.

McGraw-Hill Book Co., Inc.
\$1.00 $5\frac{3}{4} \times 9\frac{1}{8}$; viii + 121 New York

FISCHEREIBIOLOGIE DER ALPEN-
SEEN. *Die Binnengewässer. Band X.*

By Oskar Haempel.

E. Schweizerbart'sche Verlagsbuchhandlung
27.50 marks (paper) Stuttgart

29 marks (cloth) $6\frac{3}{4} \times 10$; viii + 259

OBSERVATIONS ON SOME WYOM-
ING BIRDS. *Scientific Publications of the*

*Cleveland Museum of Natural History,
Vol. I, No. 2.*

By Arthur B. Fuller and B. P. Bole, Jr.

Cleveland Museum of Natural History
75 cents Cleveland

$6\frac{3}{8} \times 9\frac{1}{4}$; 44 + 10 plates (paper)

A NEW GENUS OF AFRICAN STAR-
LINGS. *Scientific Publications of the Cleve-
land Museum of Natural History Vol. I, No. 3*

By Harry C. Oberholser.

Cleveland Museum of Natural History
50 cents Cleveland

$6\frac{1}{4} \times 9\frac{1}{4}$; 2 pages + 2 plates (paper)

NOTES ON A COLLECTION OF BIRDS
FROM ARIZONA AND NEW MEXICO.

Scientific Publications, Vol. I, No. 4.

By Harry C. Oberholser.

Cleveland Museum of Natural History
75 cents $6\frac{3}{8} \times 9\frac{3}{8}$; 42 (paper) Cleveland

REVISION OF THE FISHES OF THE
FAMILY LIPARIDAE. *Smithsonian In-
stitution. United States National Museum.
Bulletin 150.*

By Victor Burke.

U. S. Government Printing Office
45 cents Washington

$6 \times 9\frac{1}{2}$; xii + 204 (paper)

BIOLOGICAL PRINCIPLES IN GEN-
ERAL ZOOLOGY. *A Laboratory Manual.*
By H. J. Van Cleave, H. R. Linville, and
H. A. Kelley. *Ginn and Company*

80 cents $7\frac{3}{4} \times 10\frac{3}{8}$; vi + 185 Boston

ANIMAL MICROLOGY. *Practical Ex-
ercises in Zoölogical Micro-Technique.*

By Michael F. Guyer, with a chapter on
Drawing by Elizabeth A. (Smith) Bean.
Third Edition.

University of Chicago Press
\$3.00 $6 \times 8\frac{3}{4}$; xiv + 303 Chicago

BOTANY

PHYSIOLOGY AND BIOCHEMISTRY OF BACTERIA. *Volume II. Effects of Environment upon Microorganisms. Vol. III. Effects of Microorganisms upon Environment. Fermentative and Other Changes Produced.*
By R. E. Buchanan and Ellis I. Fulmer.

The Williams and Wilkins Co.

Each volume \$7.50
All three volumes, ordered at one time, \$20.00

$5\frac{7}{8} \times 8\frac{1}{2}$; Vol. II, xvii + 709

Vol. III, xv + 575

Volumes II and III complete the extensive work, as originally planned by the authors, of compiling and systematizing the great mass of data pertaining to the physiology of microorganisms. Volume I, dealing with *Growth Phases; Composition and Biophysical Chemistry of Bacteria and their Environment; and Energetics*, has previously been mentioned in these columns. Volume II, devoted primarily to a discussion of the effects of physical and chemical environment upon microorganisms, particularly bacteria, yeasts and molds, is divided into three sections, namely: (1) Effects of environment; their recognition and measurement; (2) Effects of physical environment upon microorganisms; (3) Effects of chemical environment upon microorganisms. In Volume III, the chemical transformations produced by microorganisms are discussed under the headings of (1) Special physiological interrelationships of microorganisms and (2) Effect of microorganisms upon their chemical environment. Both volumes are well documented. Each contains illustrations, a literature list of several hundred titles, subject and author indices as well as an index to microorganisms. To those engaged in the study of general biology as well as bacteriologists this completed work will be indispensable. It is a

notable contribution to American biological scholarship.



THE PRINCIPLES OF BACTERIOLOGY AND IMMUNITY. *In two volumes.*

By W. W. C. Topley and G. S. Wilson.

William Wood and Co.

\$15.00 net
per set

New York

$6\frac{1}{2} \times 9\frac{1}{2}$; xlv + 1300

It has been the aim of the authors to supply a text-book for those advanced students of medicine and biology who wish to make a comprehensive study of bacteriology and in particular its application to the problems of infection and resistance. Parts I and II, of Volume I, deal with the general and systematic aspects of the subject, while Parts III and IV, of Volume II, are devoted to "Infections and Resistance," and the "Application of Bacteriology to Medicine and Hygiene." The work bears evidence of much labor and meticulous care in its preparation. It is adequately illustrated. Reference lists, frequently lengthy, are appended to each chapter. There is an excellent index for each volume.



COMPARATIVE STRENGTH PROPERTIES OF WOODS GROWN IN THE UNITED STATES. *United States Department of Agriculture Technical Bulletin No. 158.*
By L. J. Markwardt.

U. S. Government Printing Office

10 cents

Washington

$5\frac{3}{4} \times 9\frac{1}{8}$; 39 (paper)

This bulletin is based in part upon an earlier publication issued by the U. S. Department of Agriculture on "Mechanical properties of woods grown in the United States." It gives comparative figures for weight, shrinkage and strength of 164 native species, explanations of the

eleven different tests made, and their applicability. For those who wish additional information concerning the use and derivation of the figures given there are three appendices under the following headings: (a) "Strength of structural material," (b) "Method of computing comparative strength and shrinkage figures," and (c) "Significance of variability." Seven tables are included in the text, together with formulae for calculating various strength properties. There is a brief literature list.

GNETALES.

By H. H. W. Pearson. *The Macmillan Co.*
\$6.00 7 x 10 $\frac{1}{4}$; vii + 194 New York

This monograph on a curious class of plants, posthumously published, and edited by A. C. Seward, concludes that the relationship of the three genera composing it to each other and to other groups is still obscure but "that in spite of the appearance in them of certain Angiosperm characters, they are essentially Gymnosperms."

THE PROTEASES OF PLANTS. A Record and a Reply.

By S. H. Vines. *Macmillan and Co.*
1 shilling net London and New York
5 $\frac{3}{8}$ x 8 $\frac{1}{2}$; 32 (paper)

A summary of the author's work on plant enzymes and a defense, as against Willstätter, of his conclusion that two enzymes are involved in the digestion of protein by plant-extracts.

BACTERIOLOGY. A Text Book on Fundamentals.

By Stanley Thomas. *McGraw-Hill Book Co., Inc.*
\$3.00 5 $\frac{3}{4}$ x 9; xv + 301 New York

A second edition entirely rewritten but maintaining the plan of the first edition. There is an additional chapter on the morphology and physiology of bacteria.

THE OEDOGONIACEAE. *A Monograph Including all the Known Species of the Genera Bulbochaete, Oedocladium and Oedogonium.*
By Lewis H. Tiffany. *Lewis H. Tiffany*
\$4.00 (paper) Columbus, O.
\$5.00 (cloth)

6 $\frac{3}{4}$ x 10; 253

It is hoped that this excellent monograph will be followed by similar ones on other groups of filamentous algae.

ACTA FORESTALIA FENNICA 35 and 36.

6 $\frac{3}{8}$ x 9 $\frac{1}{2}$; 464 and 506

SILVA FENNICA 13. *Om Skogars Skötsel i Norden.*

By C. C. Bocker.

6 $\frac{1}{2}$ x 10; 129

SILVA FENNICA 14. *A Short Account of the History of the Forestry of the Jokioinen Estate.*

By O. Tähtinen.

6 $\frac{1}{4}$ x 9 $\frac{3}{4}$; 50

SILVA FENNICA 15. *Wesen und Bedeutung der Waldtypen.*

By A. K. Cajander.

6 $\frac{1}{4}$ x 9 $\frac{3}{4}$; 66

SILVA FENNICA 16. *The Promotion of Higher Education in Agriculture and Forestry in Suomi.*

6 $\frac{1}{4}$ x 9 $\frac{3}{4}$; 92

COMMENTATIONES FORESTALES 3. *Neue Waldsaatmethode (Vorläufige Mitteilung).*

By K. Melders.

6 $\frac{1}{4}$ x 9 $\frac{3}{4}$; 16

COMMENTATIONES FORESTALES. *Le Prof. Dr. A. K. Cajander et ses Mérites Scientifiques dans le Domaine de la Typologie*

Forestière. (A l'Occasion du Cinquantième Anniversaire de sa Naissance.)

By Jean Miklaszewski.

$6\frac{1}{4} \times 9\frac{3}{4}$; 22

*Society of Forestry in Suomi
Helsingfors, Finland*



A TEXTBOOK OF BOTANY. Revised for Colleges and Universities. Vol. I, Morphology. Vol. II, Physiology.

By John M. Coulter, Charles R. Barnes and Henry C. Cowles.

American Book Co.

\$1.80 net for each volume *New York*

$5\frac{1}{2} \times 8\frac{1}{4}$; Vol. I, viii + 310

Vol. II, viii + 307



COLLEGE BOTANY. With Special Reference to Liberal Education.

By George B. Rigg.

Lea and Febiger

\$4.00 net $5\frac{1}{4} \times 7\frac{3}{4}$; 442 *Philadelphia*



BACTERIOLOGY. For Students in General and Household Science. Third Edition.

By Estelle D. Buchanan and Robert E. Buchanan.

The Macmillan Co.

\$3.00 $5 \times 7\frac{3}{4}$; xvi + 532 *New York*



MORPHOLOGY

AN INTRODUCTION TO VERTEBRATE EMBRYOLOGY.

By H. L. Wieman.

McGraw-Hill Book Co., Inc.

\$4.00 $5\frac{3}{4} \times 9$; xi + 411 *New York*

This book is especially designed for premedical students but will be found useful in general courses in embryology. While mainly concerned with chick and pig embryos, much attention is given to general cytology, cleavage and early stages in *Amphioxus* and the frog, and organogenesis in the human embryo.

The comparative point of view is maintained throughout the text. The many illustrations are well executed and there is a bibliography and an index.



LES PLEXUS CHOROÏDES. *Anatomie, Physiologie, Pathologie.*

By Nathalie Zand.

Masson et Cie

22 francs

Paris

$6\frac{1}{2} \times 10$; viii + 140 (paper)

In this careful monograph the author concludes that the choroid plexuses secrete the cerebrospinal fluid and serve with the meninges as a protective barrier against harmful substances dissolved in the blood. She does not find grounds for supporting the opinion of von Monakow that lesions of the choroid plexuses are the cause of schizophrenia.



VERTEBRATE EMBRYOLOGY. *A Textbook for Colleges and Universities.*

By Waldo Shumway.

John Wiley and Sons, Inc.

\$3.75 net $5\frac{7}{8} \times 9$; x + 311 *New York*

A second, revised edition of a widely used text book.



LABORATORY GUIDE TO VERTEBRATE DISSECTION. *For Students of Anatomy.*

By A. B. Appleton. *The Macmillan Co.*

\$2.40 $4\frac{3}{4} \times 7\frac{1}{4}$; xix + 152 *New York*

The price of this book as given in Volume V, Number 4, page 480, of THE QUARTERLY REVIEW OF BIOLOGY, is incorrect.



PHYSIOLOGY AND PATHOLOGY

SOME ASPECTS OF THE CANCER PROBLEM. *An Account of Researches into*

the Nature and Control of Malignant Disease Commenced in the University of Liverpool in 1905, and Continued by the Liverpool Medical Research Organization (Formerly the Liverpool Cancer Committee), Together with Some of the Scientific Papers that Have Been Published. Edited by W. Blair Bell.

William Wood and Co.

\$20.00 $7\frac{1}{4} \times 10\frac{3}{8}$; xiv + 543 New York

This book consists largely of a collection of previously published papers by Bell and his co-workers, embedded in an editorial stroma. The working hypothesis on which their researches have been based is that malignant growths are a reversion of normal tissue to a type resembling the chorionic epithelium. This is indicated by histological, chemical and physiological likenesses. Since lead has "an almost specific action on the chorionic epithelium," its effect on malignant tumors was tried. Of 566 cases treated, 304 "received more than one-half of the minimum treatment advised," and in 65 cases, or 21 per cent of the 304, the disease was completely arrested or believed cured. Bearing in mind "the serious type of case for the most part treated," Bell considers this an encouraging result. There is a bibliography of 665 titles and an index.



REFLEX ACTION. *A Study in the History of Physiological Psychology.*

By Franklin Fearing.

The Williams and Wilkins Co.

\$6.50 6 x 9; xiv + 350 Baltimore

A book of much interest and importance. The author divides the history of the development of the reflex arc concept into five periods, as follows: the pre-scientific period, the speculative period, the period of nascent experimentation, the period of the development of knowledge regarding the structural com-

ponents of the reflex arc, and the modern period. The first eleven chapters deal with the first four periods while the last five chapters deal with the fifth period. Only those phases of the subject are discussed which are related directly to reflex action as an explanatory principle in physiological psychology. The work includes a bibliography of 554 titles, and name and subject indices.



AN ELEMENTARY COURSE IN GENERAL PHYSIOLOGY. *Part I—Principles and Theory*, by G. W. Scarth. *Part II—Laboratory Exercises*, by F. E. Lloyd and G. W. Scarth.

John Wiley and Sons, Inc.

\$2.75 $5\frac{3}{4} \times 9$; xxi + 258 New York

This excellent introduction to the physiology of plant and animal life is the outgrowth of a series of laboratory exercises used by the author in a course in general physiology. The book will be found highly useful in general biology and pre-medical courses. It is divided into two parts. The principles and theory of the general properties and behavior of cells are discussed in the first part. Suggested readings for more exhaustive studies of the topics discussed are given for each chapter. The second part of the book is devoted to exercises for laboratory work. It is so arranged that some of the more advanced work can be easily eliminated. The book is illustrated and indexed and includes a section on apparatus and materials.



IMMUNITY IN INFECTIOUS DISEASES.

By A. Besredka. *Authorised Translation by Herbert Child.*

The Williams and Wilkins Co.

\$5.00 $5\frac{1}{2} \times 8\frac{1}{2}$; vii + 364 Baltimore

The author of this book, widely known

for his researches on vaccines, prefers to present his work in the form of "A Series of Studies," since the rapid progress of the science of immunity is so constantly producing new discoveries and theories. The fifteen chapters deal with experimental problems and results covering a period of thirty years work at the Pasteur Institute bearing on different aspects of the general problem of immunity. Much space is devoted to discussing critically the value of the researches of various investigators and the bearing which these have had upon the development of the science of immunity. A valuable and stimulating book to place in the hands of students who wish to do general reading in this field. It is well documented.



BREAD. *A Collection of Popular Papers on Wheat, Flour and Bread.*

By Harry Snyder. With Biographical Sketch by Andrew L. Winton.

The Macmillan Co.

\$2.50 $5\frac{1}{8} \times 7\frac{3}{4}$; x + 293 New York

A collection of papers boosting white flour and bread. The author was at one time professor of agricultural chemistry in the University of Minnesota, and was later associated with a flour-milling concern in Minneapolis. Reginald, the office boy, says that he likes white bread better, too, and has been memorizing passages for use in arguing with his mother, who is a great believer in vitamins and things.



MAMMALIAN PHYSIOLOGY. A

Course of Practical Exercises. A New Edition.

By E. G. T. Liddell and Sir Charles Sherrington.

Oxford University Press

\$4.00 $8 \times 10\frac{7}{8}$; xii + 162 New York

A series of experiments on decapitate or decerebrate mammalian preparations,

which should offer a welcome change from the plague of frogs. The book is excellently done; the illustrations are much better than we are accustomed to in a laboratory manual; the instructions are clear and helpful; and the annotations should give the student an historical orientation of value.



MEDICAL AND SURGICAL YEAR-BOOK. *Physicians Hospital of Plattsburgh. Comprising Wednesday Afternoon Invitation Lectures, Papers of the Cardiac Round Table, The First Beaumont Lecture, Collected Papers by the Staff.*

The Superintendent, Physicians Hospital of Plattsburgh
Plattsburgh, N. Y.

\$3.50

$6 \times 9\frac{1}{4}$; xv + 322

A collection of lectures and papers, largely on cardiovascular-renal diseases, but also including an address at the unveiling of a memorial tablet to Dr. William Beaumont, and papers on pneumonia, congenital syphilis, gall-bladder disease, adrenal insufficiency, pulsating exophthalmos, pathologic labor, gas bacillus infection, pulmonary cancer, anesthetics, x-ray examination of teeth, gastric ulcer and carcinoma, bronchoscopy, and agranulocytic angina.



REVIEW OF CARBON MONOXIDE POISONING. *Public Health Bulletin No. 195.*

By R. R. Sayers and Sara J. Davenport.

U. S. Government Printing Office

20 cents

Washington

$5\frac{3}{4} \times 9\frac{1}{8}$; iii + 97 (paper)

This survey deals with the occurrence and symptoms of carbon-monoxide poisoning; its diagnosis; the percentages of carbon-monoxide dangerous to breathe, and the pathology, prevention and treat-

ment of carbon-monoxide poisoning. There is a bibliography of 195 titles.



SENSATION AND THE SENSORY PATHWAY.

By John S. B. Stopford.

Longmans, Green and Co.

\$3.00 $5\frac{1}{2} \times 8\frac{1}{2}$; xii + 148 New York

An account of our present knowledge of the sensory paths and centers of the peripheral and central nervous system.



LA RATE. *Organe Réservoir.*

By Léon Binet.

Masson et Cie

20 francs $6\frac{1}{8} \times 9\frac{1}{4}$; 117 (paper) Paris

An experimental study of the functions of the spleen, especially as a blood reservoir.



LABORATORY MANUAL IN COLLEGE PHYSIOLOGY.

By Cleveland P. Hickman. The Macmillan Co.

\$1.10 $5 \times 7\frac{1}{2}$; xiv + 116 New York



BIOCHEMISTRY

THE MATERIALS OF LIFE. *A General Presentation of Biochemistry.*

By T. R. Parsons.

W. W. Norton and Co., Inc.

\$3.00 $5\frac{3}{4} \times 8\frac{1}{4}$; 288 New York

As this interesting exposition of biochemistry is aimed at the general reader, it is written without using chemical formulas. The greater part of the book deals with nutrition, but there are also chapters on the chemistry of muscular exercise, blood chemistry, vitamins, endocrine secretions, and the cycle of nature. There is a list of suggested reading and an index.

NEWTON, STAHL, BOERHAAVE ET LA DOCTRINE CHIMIQUE.

By Hélène Metzger.

Félix Alcan

40 francs $5\frac{1}{2} \times 9$; 332 (paper) Paris

An account and examination of the chemical theories of Newton, Stahl, and Boerhaave, written largely with a view to establishing their relations to Lavoisier. The book is a valuable contribution to the history of chemistry. The index is noteworthy in that it supplies a line or two of biographical information about the authors cited.



DIE GLOBULINE.

By Mona Spiegel-Adolf.

Theodor Steinkopff

33 marks (paper)

Dresden

35 marks (cloth)

$6\frac{1}{4} \times 9\frac{1}{4}$; xv + 452

This exhaustive monograph, the fourth volume of the *Handbook of Colloid Science* edited by W. Ostwald, treats the chemistry, physical chemistry, and biological and medical aspects of this important class of proteins.



INTRODUCTION TO PHYSIOLOGICAL CHEMISTRY.

By Meyer Bodansky.

John Wiley and Sons, Inc.

\$4.00 $5\frac{3}{4} \times 9$; ix + 542 New York

A second edition, rewritten and enlarged. Two new chapters have been added, one dealing with the composition of food stuffs and the other with the composition of milk and certain tissues.



DIE CHEMIE DER CEREBROSIDE UND PHOSPHATIDE.

By H. Thierfelder and E. Klenk.

Julius Springer

19.60 marks (paper)

Berlin

21.20 marks (bound)

$5\frac{1}{2} \times 8\frac{1}{2}$; viii + 224

This monograph on two important classes of lipoids will be useful to the biochemist.



SEX

GENERATIONS OF ADAM.

By A. L. Wolbarst. *Newland Press*
\$3.50 $5\frac{1}{2} \times 8$; ix + 355 New York

This is a book which no Christian mother should put in the hands of her child. Its point of view is indicated by its preface: "It aims to emphasize the sharp line of demarcation between the biology of sex as ordained by Nature, or God, as you prefer, and the religious or moral concept of sex so vigorously and tenaciously fostered by theology; it seeks to eliminate from our social consciousness the doctrine that sex and sin are synonymous and inseparable,—in other words, to divorce sin from sex."

The author has attempted to treat his subject realistically and rationally. The result is vastly superior to most of what gets into print about sex in books designed for the general public.



THE INTERNAL SECRETIONS OF THE OVARY.

By A. S. Parkes. *Longmans, Green and Co.*
\$7.50 $5\frac{3}{4} \times 8\frac{5}{8}$; xv + 242 New York

In this book the author brings together the more important facts bearing upon the internal secretions of the ovary. Considerable space is devoted to the morphological aspects of the oestrous cycles in those species where it has been studied in some detail. In the sections dealing with the endocrine control of the female reproductive organs the author gives a very complete discussion of the various phases of the problem, including much experimental data. A valuable

part of the monograph is the bibliography of 661 titles. The work includes many excellent illustrations and tables and diagrams of growth curves and oestrous cycles. There are author and subject indices. Students and investigators interested in the physiology of the endocrine organs will find this a notable addition to the literature of their field.



BIOMETRY

INTRODUCTION TO MEDICAL BIOMETRY AND STATISTICS.

By Raymond Pearl. *W. B. Saunders Co.*
\$5.50 net $6 \times 9\frac{1}{8}$; 459 Philadelphia

This second edition of this well-known textbook is revised and enlarged, and to a considerable extent rewritten in the light of seven years' experience of its use in the class-room. Among the additions are a section on the nature of statistical knowledge; a more detailed discussion of the census method; the fourth decennial revision (1929) of the International List of Causes of Death, including the Intermediate and Abridged Lists and recommendations of the International Commission; sections on the making of scientific records; record forms; a life table nomogram; applications of the corrected rate principle; a more detailed treatment of the chi-square test; the graphic representation of relative variability; and a chapter on the logistic curve.



THE GREAT MATHEMATICIANS.

By H. W. Turnbull. *Methuen and Co., Ltd.*
2s. 6d. $4\frac{1}{8} \times 6\frac{7}{8}$; viii + 128 London

A brief account of some of the great mathematicians. The author has attempted to tell the story without the use of mathematical symbolism, and has, on the whole, succeeded surprisingly well.

Naturally, perhaps, the best chapters are the earlier ones, and especially those dealing with the Greeks; it is much less difficult to give a popular account of elementary geometry than of the geometry of Riemann. In general, the names which appear are well chosen, though omissions will probably occur to many readers. For example, the relation of Barrow to Newton and the differential calculus is completely passed over.



PSYCHOLOGY AND BEHAVIOR

HUMAN SPEECH. *Some Observations, Experiments, and Conclusions as to the Nature, Origin, Purpose and Possible Improvement of Human Speech.*

By Sir Richard Paget.

Harcourt, Brace and Co.

\$6.00 5½ x 8½; xiv + 360 New York

The more interesting and important portions of this book are those dealing with the author's experimental researches into the nature of speech sounds. He has succeeded in producing artificially nearly all the sounds of English speech, both consonant and vowel. He finds that both consonants and vowels are essentially double resonance phenomena, the consonants being also characterized by the change and rate of change of pitch produced by alterations in one of the orifices of the resonators.

When he comes to deal with the origin of speech, he is on less firm ground. He holds to the "gesture theory" of the origin of speech—that is, that speech originated in lingual and buccal gestures simultaneous with and imitative of manual gestures. Whether this is the true origin of speech we do not profess to know; but we feel that the evidence here offered is wholly inadequate to establish its plausibility.

DIRECTION ORIENTATION IN MAZE RUNNING BY THE WHITE RAT.

Comparative Psychology Monographs, No. 32.
By J. F. Dasbiell.

The Johns Hopkins Press

\$1.50 6¾ x 10; 72 (paper) Baltimore

An important contribution to studies in animal learning. The rats in these experiments exhibited a "general orientation function" which successfully served them in solving their problems of maze running. The author found that

Instead of learning one pathway-pattern to the goal by the often-stated process of (a) chancing upon a certain way that turned out to be adaptive or successful and then (b) fixating this way by tending to repeat it more and more—our animals *learned to become adjusted in some more general manner, directionally*, which more general adjustment then served as a *steering or influencing factor operative somewhat independently of the purely local stimuli encountered by the rat and so serving to guide it even when tracing pathways never before entered.*

Various contemporary studies and theories are examined and discussed by the author in seeking an interpretation of these results but, none seeming adequate, the following suggestion is offered as a possible explanation.

When a rat first enters the maze there may be set up some kind of kinesthetic or organic posturing or set (developed in preceding trials), determined by the animal's position when proceeding up the entrance passage way. Then, as the animal traverses the maze and encounters obstacles forcing it to turn right or left, a persisting segment of the initial orientation may inhibit specific stepping movements antagonistic to it and facilitate those consonant with it.

The report includes illustrations of rat performance in maze routes, tables of runs, etc. and a bibliography.



PREFERENTIAL MANIPULATION IN CHILDREN.

Comparative Psychology Monographs, No. 33.

By *Julia H. Heinlein.*

The Johns Hopkins Press
\$1.75 7 x 10; 121 (paper) *Baltimore*

In this investigation on 36 children of pre-school age at the Child's Institute of the Johns Hopkins University, the author states that the results

of the various tests of handedness seem to indicate the existence of "degrees" of manual bias ranging from a pronounced preference for either the right hand or the left hand, to a relatively ambidextrous state in which neither hand is definitely favored, or in which the hand "convenient" under the circumstance is favored. The two manual types designated conventionally as "right-handed" and "left-handed" apparently indicate "trends" rather than two distinct classes, at least in so far as activities of the type used in these tests are concerned.

It is interesting to note that there was marked indication that the training gained in a series of practice tests for the non-preferred hand in a group of "right-handed" children was transferred when the tests were presented to the same children for "right-handed" performance. On the other hand

performances of the majority of the children in the left-handed group did not show a marked tendency toward improvement in either the practiced right hand or the unpracticed left hand, although there was some individual variation.

In addition to the manual tests, the preferential use of hands by the children of the pre-school group was daily under observation and yielded significant results. The author includes in her report tables showing the results of the tests and a bibliography of 16 titles.



SYSTEMATIC PSYCHOLOGY: PROLEGOMENA.

By *Edward B. Titchener.*

The Macmillan Co.
\$2.50 4 $\frac{7}{8}$ x 7 $\frac{3}{8}$; xi + 278 *New York*

Although only a fragment of what the

author intended to be his *magnum opus*, this book is an important contribution to the foundations of psychology. In formulating his definition of psychology Professor Titchener found it necessary to consider the essential character of science in general and of physics and biology in particular. The definitions of the three sciences at which he arrives are as follows:

Psychology is the science of existential experience regarded as functionally or logically dependent upon the nervous system (or its biological equivalent);

Biology is the science of existential experience regarded as functionally or logically dependent upon the physical environment; and

Physics (including chemistry and physical chemistry) is the science of existential experience regarded as functionally or logically interdependent.



THE MEANING OF SACRIFICE. *Thesis Approved for the Degree of Doctor of Philosophy in the University of London. The International Psycho-Analytical Library No. 16.*

By *R. Money-Kyrle.* *The Hogarth Press*
18 shillings 6 $\frac{1}{4}$ x 9 $\frac{1}{2}$; 273 *London*

The author finds Freud's theory of the origin of sacrificial rites from the Oedipus complex a more adequate explanation of the different forms of sacrifice actually observed than other theories. He points out, however, that the assumption of the inheritance of acquired memory made by some of Freud's followers is both dangerous and unnecessary. "Sacrifice may be regarded, less as the result of a primeval crime, than as the symbolic expression of an unconscious desire for parricide which each individual has himself acquired."



THE GROWING BOY. *Case Studies of Developmental Age.*

By *Paul H. Furfey.* *The Macmillan Co.*
\$2.00 5 x 7 $\frac{1}{2}$; ix + 192 *New York*

Doctor Furfey gives here the results of his studies of the personality and interests

of boys from six to sixteen years old. He finds a normal development from the dramatic play of the six-year-old through the gang age (from ten to fourteen) to adolescence. There are, however, individual variations in the rate of this development which lead him to the concept of developmental age. Thus a boy of ten who retains the play activities characteristic of the eight-year-old has a developmental age of eight and a developmental quotient of 80. Developmental age is not correlated with mental age, but there is a small correlation with weight and height.



READINGS IN PSYCHOLOGY.

By Raymond H. Wheeler. With special readings by Harry Helson, Milton Metfessel and Thomas D. Cutsforth.

Thomas Y. Crowell Co.

\$3.75 $5\frac{1}{2} \times 8\frac{1}{2}$; x + 597 New York

A collection of papers, designed for collateral reading for a first course in psychology. The papers, largely experimental in character, are selected to illustrate and support the "organismic" view of the editor, which seems to be fundamentally that of the Gestalt school.



NINTH INTERNATIONAL CONGRESS OF PSYCHOLOGY, Held at Yale University, New Haven, Connecticut, September 1st to 7th, 1929, under the Presidency of James McKeen Cattell. Proceedings and Papers.

The Psychological Review Co.

\$5.25 $7 \times 10\frac{1}{4}$; xli + 534 Princeton, N. J.

Contains abstracts of papers read, together with addresses by various officials of high degree.



DE OMNIBUS REBUS ET QUIBUSDEM ALIIS

NEW FRENCH COOKING. 300 New and Unique Recipes.

By Paul Reboux. Translated from the French by Elizabeth Lucas. Alfred A. Knopf, Inc.

\$2.50 $5 \times 7\frac{1}{2}$; xiii + 263 New York
FRENCH COOKING FOR ALL.

By Gaston Voisin. Frederick A. Stokes Co.

\$2.00 $5 \times 7\frac{3}{8}$; 187 New York

There appears to be a considerable present interest on the part of the great American public in French food and cooking, if one may judge from the activity of publishers in catering to it. What is the cause of so noble an elevation in the public taste above the hitherto current hog and hominy, pork and beans, and baking powder biscuit level of gastronomy has not been revealed, but in any case it is worthy of all praise and pious giving of thanks to God and Brillat-Savarin.

The two books before us lie at the opposite poles of merit. M. Reboux's treatise is probably the most original and entertaining work on gastronomy to appear in English, while M. Voisin's (there is no evidence of any connection with the illustrious *restaurateur* of that name) is nearly worthless. The measure of its authoritativeness is given by the fact that it solemnly describes the preparation of *champignons à la Provençale* without any mention of garlic at any stage! No more need be said of such a misleading, debased, pernicious, and futile book.

Paul Reboux is one of the most original and versatile of living Frenchmen. He has been a poet, a newspaper editor (*Paris-Soir*), a political writer, a columnist,—all with brilliant success. His post-war book *Les Drapeaux* was, in our opinion, the soundest and most penetrating book ever written on patriotism. If the advice he gave in it had been heeded the story of Europe during the decade just passed would have been a very different one. Now he appears as a *gastronome*. This book is delightful. His recipes are adorned with brilliantly witty comment, and they are of an originality. Food and

drink are, of course, preeminently matters of taste, upon which universal agreement is neither to be expected nor desired. We, for example, while observing much in Reboux's gastronomic philosophy that is admirable, cannot follow him in his passion for bananas, a food obviously intended by the Almighty for *Drosophila* but not for man. But on the other hand his ideas about the making of a duck *pâté* are plainly inspired.

No biologist (or other civilized person) should be without this book.



TYPES OF PHILOSOPHY.

By William Ernest Hocking.

Charles Scribner's Sons

\$2.50 5½ x 8½; xv + 462 New York

"Every instructor, whatever his subject, conveys a philosophy; the teaching of English, of history, of economics, of science is at the same time a teaching of philosophy, if only because the instructor is a man and cannot help communicating himself *via* his subject." Hocking has prepared a valuable summary and discussion of the types of philosophy for the thinking man and for the beginner in the study of philosophy. In this book the author combines the historical with the systematic treatment of the subject. There is a careful selection of the types of philosophy from the standpoint of "the validity of the world view, not in the historic rôle." This makes the book valuable not only for the beginner but also for the seasoned student of philosophy and for the scientist, because it presents an argument in the sequence of types, which, in its simplicity of presentation, preserves "first Principles." The chief types of philosophy discussed are spiritualism, naturalism, pragmatism, intuitionism, dualism, idealism, realism, and mysticism,

in the order named. They are offered as philosophies contributing towards a synthetic world view rather than as competing systems of philosophic thought. This approach is especially useful for the scientist and teacher, who wishes to orient his thinking in relation to his field of science, and to assist in clarifying his concepts toward a synthetic philosophy of his own. Hocking closes with his own *confessio fidei*. This book is well worth the consideration of the biologist. There are lists of numerous, selected references, classified for student use, accompanying the discussion of each type. Subject and name indexes are printed separately.



A PRACTICAL MEDICAL DICTIONARY of Words Used in Medicine with Their Derivation and Pronunciation, Including Dental, Veterinary, Chemical, Botanical, Electrical, Life Insurance and Other Special Terms; Anatomical Tables of the Titles in General Use, and Those Sanctioned by the Basle Anatomical Convention; Pharmaceutical Preparations, Official in the U. S. and British Pharmacopoeias and Contained in the National Formulary, and Comprehensive Lists of Synonyms.

By Thomas L. Stedman.

William Wood and Co.

\$7.50 net 6 x 9½; xi + 1220 New York



SHORT TALKS ON SCIENCE.

By Edwin E. Slosson. The Century Co.
\$2.00 5 x 7¼; xii + 281 New York

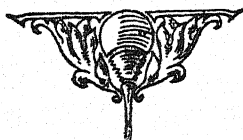
A collection of brief notes, largely reprinted from the weekly journals, touching on topics from bacteriology to physics. It reminds us strangely of Mr. Ripley's "Believe it or not," but others may differ.

THE REVOLT AGAINST DUALISM.
An Inquiry Concerning the Existence of Ideas.
By Arthur O. Lovejoy.

W. W. Norton and Co., Inc.
\$4.00 6 x 9; xii + 325 New York

In this analysis of the realistic-monistic
movements of the past quarter century,
Dr. Lovejoy concludes that they are

either inadequate or essentially dualistic
under the disguise of a novel terminology.
If this distinguished author would only
write as simply, lucidly, and forcefully as
he speaks, this important book would be
assured of a wider audience than it will
probably get.



THE QUARTERLY REVIEW of BIOLOGY



ANALYSIS OF INTERSEXUALITY IN THE GIPSY-MOTH

By RICHARD GOLDSCHMIDT

Berlin-Dahlem

DURING the past twenty years I have, with a number of collaborators, analyzed the phenomenon of intersexuality in the gipsy-moth, *Lymantria dispar* L. A few smaller contributions have been added by such authors as Kosminsky, Lenz, Schweitzer, Standfuss. This work is now practically finished, at least as far as I am concerned, and I believe that every important point has been sufficiently worked out, though minor gaps are certainly left. The long time over which this work extended necessarily led to certain changes in our views, as work progressed, as well as to corrections of experimental data with increasing bulk of evidence—both of which make the study of the original papers still more laborious than is already the case on account of the mass and complexity of the facts. A review of the whole work, as it stands to-day is therefore probably not out of place. The innumerable moths which have been bred in these experiments have been preserved and are available for study or control in our laboratory. The genetic side of the work will be reviewed more

thoroughly than the more easily accessible morphological and general work.

INTRODUCTION

Intersexuality in the gipsy-moth is a phenomenon which occurs entirely within the normal chromosome behavior. It might therefore be described as diploid intersexuality. (For exceptions see later, non-disjunction.) The gipsy-moth shows like other Lepidoptera the *Abraxas* type of sex-chromosomes (female heterogamety) which is clearly demonstrated by the intersexuality experiments. Cytologically an X-Y group could thus far not be distinguished and among the mutations studied by me and Machida no sex-linked character appeared. In the next relative of the gipsy-moth, the nun moth *Lym. monacha*, an X-Y group exists in the female (Seiler) and sex-linked inheritance of the *Abraxas* type was found (Goldschmidt). Intersexuality is produced in an absolutely orderly way by crossing different geographic races of this moth. Occasionally intersexual specimens are found in nature within a pure race and recently Kosminsky (52) has discovered and studied

a case where within a pure Russian race lines could be isolated which regularly threw intersexes. We shall refer later to this exceptional phenomenon, which had never occurred among the pure strains of numerous races which I bred in innumerable numbers.

The intersexual individuals or intersexes are of two main types, which are called female and male intersexes respectively. These names are convenient though not logically correct. What is meant is that female intersexes are XY-individuals which ought to be females, if only the chromosome set were decisive; male intersexes are correspondingly XX-individuals. Intersexes represent macroscopically a definite stage between the two sexes and male and female intersexes can be distinguished at first sight. Closer inspection shows that an intersex represents a strange mixture of the individual female and male characters, which are combined in a certain orderly way. Therefore in the beginning of our work (1911-15) we used the term gynandromorphs for these types, though emphasizing their difference from typical gynanders. Since 1915 we introduced the term intersexes and clearly defined the difference between gynandromorphism and intersexuality. Female as well as male intersexes in different types appear again according to definite laws representing the different degrees of intersexuality, characterised by the relative amounts of female and male structures. Thus a series of female intersexuality can be found beginning with normal females and leading through increasing grades of intersexuality (increasing of male admixtures) to complete sex-reversal i.e. normal functioning males of XY-constitution. A corresponding series of male intersexuality leads from a normal male through all the grades of male intersexuality to a sex-reversal—female. The

simple law which explains the structure of these different intersexes and which had first been noticed by Baltzer in the intersexes of *Bonellia*, is this: an intersex is an individual, which is developed first with its gametic (XX or XY) sex but from a certain moment in development, the turning point, completes its development with the other sex. The degree of intersexuality is therefore a function of the position of the turning point in time: earlier turning point—higher degree of intersexuality. The phenomenon of intersexuality affects all sexual characters i.e. primary and secondary sex characters—simultaneously according to the fore-mentioned law. (In my first papers (1911, 1912) I thought that only secondary characters were involved; later I could show that the primary characters were also affected simultaneously.) Therefore only general sex-genes are involved in the analysis.

THE BASIC EXPERIMENTS

Reciprocal crosses between a certain European and a certain Japanese race (which one see later) give the following results:

1. European female \times Japanese male:
All sons normal, all would-be daughters intersexual.
2. Japanese female \times European male:
Sons and daughters normal.
3. F_2 from Nr. 1 (Only possible, if lowest type of intersexuality, which alone is fertile, is obtained):
All sons normal, daughters $\frac{1}{2}$ normal, $\frac{1}{2}$ intersexual, intersexuality of the same degree as in the mother.
4. F_2 from Nr. 2:
All daughters normal, sons at least $\frac{1}{2}$ normal, up to $\frac{1}{2}$ intersexual (for this ratio see later).

This experiment leads to a convenient terminology which is free from theoretical assumptions and will be used henceforth. The Japanese race of this first experiment

is called strong and the European race weak. Female intersexuality is then produced in F_1 if a weak female is crossed with a strong male; male intersexuality appears in a part of the gametic males in F_2 of the reciprocal cross. The first experiment already shows that both sexes contain the anlagen for either sex, which can be brought to light in definite gametic combinations. It further shows that the resulting sex (including intersexuality) is dependent upon two genetic somethings, one of which shifts sex towards the female, the other towards the male side, or in other words female and male determiners. It further shows that sex is dependent upon a certain relation of these determiners, their relative strength or weakness, in other words upon a balance or unbalance of these determiners. Thus even in my first publication on this subject in 1911, the conception was introduced, which is nowadays called genic balance.

The next question is how are these strong and weak sex determiners inherited and how are the different results of reciprocal crosses to be explained? The answer, which later will be verified in most decisive tests, was derived first from the following elementary set of F_1 and F_2 combinations.

1. Crosses within the maternal weak line

COMBINATION	RESULT
F_1 weak ♀ × strong ♂...	all ♀ J (intersexual)
F_2 (weak ♀ × strong ♂) ² ...	$\frac{1}{2}$ ♀, $\frac{1}{2}$ ♀ J
backcross: weak ♀ × (weak ♀ × strong ♂) ♂...	$\frac{1}{2}$ ♀ $\frac{1}{2}$ ♀ J
backcross: weak ♀ × (strong ♀ × weak ♂) ♂...	$\frac{1}{2}$ ♀ $\frac{1}{2}$ ♀ J
backcross: (weak ♀ × strong ♂) ♀ × weak ♂...	all ♀ normal
backcross: (weak ♀ × strong ♂) ♀ × strong ♂...	all ♀ J

In all these crosses the maternal line is weak. The results show at once that the "strength" which produces female intersexuality is inherited within the X-chromosomes. We do not use the terms W and Z chromosomes in the case of female heterogamety. One of the reasons is the following: We can produce sex-reversal-males which are heterogametic, and sex-reversal-females which are homogametic. Are their respective sex-chromosomes now XY or WZ? Each female receives her single X-chromosome from the father. The results are exactly what is to be expected if this intersexuality-producing strength is a property of the X-chromosome of the strong race. It shows further that correspondingly the X-chromosome of the weak race carries the property weakness. It finally shows that the F_1 females behave like pure weak females in the hybrid combination (weak ♀ × strong ♂) × strong ♂, that is in the maternal weak line.

2. Crosses within the maternal strong line

COMBINATION	RESULT
F_1 strong ♀ × weak ♂.....	normal ♂
F_2 (strong ♀ × weak ♂) ²	$\frac{1}{2}$ ♂ $\frac{1}{2}$ ♂ J*
backcross: strong ♀ × (strong ♀ × weak ♂) ♂.....	normal ♂
backcross: strong ♀ × (weak ♀ × strong ♂) ♂.....	normal ♂
backcross: (strong ♀ × weak ♂) ♀ × strong ♂.....	normal ♂
backcross: (strong ♀ × weak ♂) ♀ × weak ♂.....	all ♂ J*

* For exact ratio see later.

This series shows: The property "weakness" of the weak males is inherited in their X-chromosomes; in these combinations two strong X-chromosomes or one strong and one weak X-chromosome produce normal ♂♂; two weak X-chromo-

somes produce intersexual ♂♂. All mothers behave as strong females, never producing female intersexuality, whether they are of pure strong race or F_1 hybrids between a strong mother and a weak father.

If we consider both series together we realize that strength and weakness are, first, properties of the X-chromosomes of the respective races and, second, properties of something inherited in the female line, i.e. maternally only; further that the resulting sex is determined by a definite relation or balance between the respective strength (or weakness) of the one type of determiners inherited maternally and the other type inherited within the X-chromosomes; further that, whereas the combination of the weak maternally inherited thing with a strong determiner in an X-chromosome shifts the would-be female towards maleness (female intersexuality) and whereas the combination of a strong maternally inherited thing with two weak determiners in the X-chromosomes shifts the would-be male towards femaleness (male intersexuality), the X-chromosomes must contain a male determiner, strong in the strong and weak in the weak races, and that the thing which is inherited maternally is a female determiner, again strong in the strong and weak in the weak races. This means that sex in the gipsy-moth is determined by a relation or balance between a maternally inherited female determiner, F, and one (♀) or two (♂) male determiners, M, inherited within the X-chromosomes. In Mendelian symbols,

$\frac{F}{M(X)} = \text{♀}$, $\frac{F}{M(X)M(X)} = \text{♂}$. It further means that the pure sexes appear, if F and M or MM are properly balanced or, in a formula, $\frac{F}{M} = \text{min} = \text{♀}$, $\frac{MM}{F} = \text{min} = \text{♂}$; that intersexes appear if by hybrid combination of F and M of not

matched relative strength F and M are not properly balanced, or in a formula $\frac{F}{M}$

$= \text{less than min} = \text{♀}$, $\frac{MM}{F} = \text{less than}$

$\text{min} = \text{♂}$ J. The minimum required to insure the complete superiority of M or F over its counterpart F or M has been termed epistatic minimum. Between the

two epistatic minima $\frac{F}{M} = +e$ and $\frac{F}{MM}$

$= -e$ the series of intersexes are situated, female intersexes in the XY animal, male intersexes in the XX animal. The results of this analysis of the elementary set of experiments have been tested with absolutely positive results in the further work.

ARE F AND M SINGLE GENES?

Already at this point of the analysis the question might be asked, whether F and M have to be considered as single genes. The answer is that never in the thousands of crosses, partly of the most complex type, was any result obtained, which would support any other conclusion; further that numerous multiple allelomorphs of F and M have been studied and that mutations of the "strength" of these genes have been observed, (see 25). Under these circumstances F and M have to be treated as single genes, if we keep within the elementary rules of genetic analysis. Occasional utterances of critics that they do not "believe" it may therefore be disregarded. But it might be worth while to uncover the basis of such beliefs, because it is found in a widespread misconception of what sex-determination means. The idea is that sexes are distinguished by so many different morphological and physiological characters that such differences could not be accounted for by a single gene difference. Such a view reveals in my opinion very loose thinking,

disregarding completely the difference between sex inheritance and other Mendelian inheritance. Every individual of a form which exhibits sexual differences, contains the necessary genetic outfit for the production of the characters of both sexes, an obvious fact, but finally proven by the phenomenon of diploid intersexuality. But in development a given group of cells, say the primordial gonocytes, or the anlagen of an antenna, has at a certain moment to decide which of the alternative possibilities of differentiation, present as "reactionsnorm" on the basis of the whole genetic constitution, will be realized. This decision is brought about by the relative condition (balance) of the F and M genes at the moment of deciding the alternative. Intersexuality definitely shows that this decision may be reversed in the same individual at consecutive moments. The viewpoint which we are discussing obviously mistakes the set of general genes which have an alternative reactionsnorm, according to the $\frac{F}{M}$ situation, for sex-determining genes. The error is the same as if somebody should conclude from the fact that a colored *Primula* has a white flower at high temperature that more than one gene was involved. The difference between the two examples is of course that in *Primula* the factors which decide the alternative are external factors, in the case of sex, however, internal factors on a genetic basis. But logically both cases are alike. Concerning modifying genes see later.

DIFFERENT TYPES OF STRONG AND WEAK RACES AND THE MULTIPLE ALLELO-MORPHS OF F AND M

Some results obtained in repeating the first experiments led to the expectation that different strong and weak races were to be found in different geographical

habitats, especially in Japan. Repeated collecting trips confirmed this expectation and the analysis of these different races has not only furnished extremely interesting results for the problem of geographic variation, which will not be discussed here, but also permitted a complete analysis of intersexuality. Races over the whole range of distribution of the gipsy-moth, i.e. over the range of the palaearctic region, many of which can also be distinguished by somatic characters, have been tested (see 41). According to their behavior in the intersexuality experiments the following types may be distinguished:

1. *Strong races.* These have strong F and M. A strong male crossed to a weak female produces in F_1 normal ♂♂ and female intersexes. The degree of intersexuality is typical for a given cross and different with different combinations of the individual strong and weak races. F_2 of the reciprocal cross throws a certain percentage (up to 50%) of male intersexes. The strong races are exclusively found in the mainland of North-Eastern Japan, the area being practically identical with that natural division of Japan which is called Kwanto. There are indications that in the mountainous districts different forms occur, but the decisive tests are not yet finished. Within this area the strength of F and M is not constant. The different tests show that generally speaking the "strength" decreases from Northeast to Southwest. A number of strong races of different strength have been tested, which e.g. means that one and the same type of weak female produces increasing grades of female intersexuality in F_1 with males of increasing strength. These results are typical and have never failed when repeating the respective crosses.
2. *Neutral races.* A female of a neutral race if crossed to a male of any race, weak or strong, produces in F_1 normal offspring.

This shows the F of the neutral race to be relatively strong. A male of a neutral race produces with all females, even with those of the weakest races, only normal offspring. This shows the M of the neutral race to be relatively weak. F_2 of the cross neutral ♀ \times weak ♂ produces a certain percentage of male intersexes, again showing the F of the neutral race strong. It will later be shown how these different strengths may be measured. The neutral races inhabit all south-western Japan, the region called Kwansai, and also the southern Island of Kyushiu (see later). Again the strength of their F and M decreases from East to West, the strongest neutrals being found near the borderline between Kwanto and Kwansai, the weakest in the island of Kyushiu. (For tests see later). Neutral races are further found in Northern Korea, Manchuria, North-Eastern China and Russian Turkestan (Central Asia). The latter exhibit the combination of a rather strong F with a rather weak M. 3. *Weak races.* These occupy all Europe. Races have been tested from Central Europe, the Alps, Italy, Spain, The Balkans, European Russia, all being weak. But in addition to these a weak race occupies the northernmost Island of Japan, Hokkaido—as a matter of fact, the weakest of all known races. Among these weak races we have to distinguish three types. 1.) a. The race Hokkaido. This race, the very weakest, is characterized by the following combinations: Hokkaido ♀ \times strong ♂ produce only males, half of which are sex-reversal-males i.e., the final type of female intersexuality. b. The combination of an F of a strong race with two M from Hokkaido, $F_{Sr} M_{Hok} M_{Hok}$, is a sex-reversal-female (for details see later). 2.) The weak races s.str. These are characterized as follows: a weak ♀ \times strong ♂ again produces only sex-reversal—♂.

The combination of a strong F with two weak M, $F_{Sr} M_w M_w$, however, is an intersexual male. Of these weak races again different degrees could be distinguished by special tests (see later). No regularity regarding their distribution in Europe could be found. 3.) The half-weak races. These occupy a position between the neutral and the weak races. A half weak ♀ crossed to a strong ♂ produces in F_1 all female intersexes (no-sex-reversal-♂), the typical degree of intersexuality,—which, however, differs in different crosses being dependent upon the relative half-weakness of the mother's race and the relative strength of the father's race. The combination of a strong with two half-weak M is an intersexual ♂ of lower intersexuality than before (No. 2). Half-weak races with absolutely irregular distribution have been found in one valley of the European Alps (Tessin). They occur also in Japan in the Island of Kyushiu at the south-western end of the neutral races and in Korea. The gipsy-moth introduced from France into New England also belonged to this type as tests made 15 years ago showed.

The description of these races shows already that by proper combination of the weak F with the strong M all degrees of female intersexuality from the first beginning to complete sex-reversal can be and have been produced in an orderly manner in 100 per cent of the would-be daughters.

Whenever by such a cross the relative weakness and strength of the F and M genes of two races has been tested, the results of crossing the same race of females with males of different races or different females with the same males may be predicted. The results of innumerable crosses always came out according to expectation. Whenever a cross for female intersexuality gave information about the type of the two races involved, the expectations for

all other hybrid combinations, especially those for producing male intersexuality, could be predicted and never a failure occurred, as the immense experimental material in our publications proves (see No. 20, 25, 28, 40, 42).

In these different crosses and still more in the complex crosses later to be discussed we had a chance to find out whether the different degrees of strength and weakness of F and M respectively were properties of the same gene or caused by additional (modifying) genes. The results always were such as would be expected if the same genes F and M were present in the different races in different condition, called here strength or weakness. In other words the different F and M of the genetically different races proved to be a series of multiple allelomorphs of F and M. The result of a given combination in regard to sex is therefore determined by the balance or unbalance between the relative strength of the present members of the F series and the M series. To give a few concrete examples:

F_{Soeul} M_{Gifu} = low grade ♀ J
 F_{Soeul} M_{Tokyo} = high grade ♀ J
 F_{Tessin} M_{Tokyo} = very high grade ♀ J
 F_{Kumamoto} M_{Tokyo} = very low grade ♀ J
 F_{Hokkaido} M_{Tokyo} = sex-reversal ♂
 F_{Kyoto} M_{Tokyo} = normal ♀
 F_{Tokyo} M_{Kyoto} M_{Kyoto} = normal ♂
 F_{Tokyo} M_{Hokkaido} M_{Hokkaido} = sex-reversal ♀
 F_{Tokyo} M_{Soeul} M_{Soeul} = very low inters. ♂
 F_{Tokyo} M_{Berlin} M_{Berlin} = medium inters. ♂
 F_{Tokyo} M_{Trentino} M_{Trentino} = very high inters. ♂

These results finally show that the different conditions of the F and M of the different races, called their weakness or strength, form an orderly, quantitative series in regard to their effect and that the different possible combinations behave exactly as if the different degrees of strength of these genes could be expressed in numerical values, which, if substituted for each other, change the effect with a

corresponding measure. This led me first to identify the relative strength or valency of these genes with their absolute quantity (17), measured in numbers of molecules. This identification will be discussed later, because the whole analysis is exactly the same, whether we speak concretely of the quantity of the genes or agnostically of their strength or valency.

TWO METHODS OF TESTING THE WHOLE CONCEPTION

The correctness of the analysis has been further tested by two methods, which furnish most decisive proofs:

a. *The substitution test for gametic males* (see 20, 25, 28, 40, 41, 42). It has been mentioned that XX-Individuals of the genetic constitution F_{strong} M_{Hok} M_{Hok} i.e. would-be males with the F of a strong race and two M of the weakest race, Hokkaido, are sex-reversal-♀, because the two M are so weak that the strong F outbalances them completely. The back cross (Tokyo ♀ × Hokkaido ♂) × Hokkaido ♂ therefore produces nothing but females, half normal, half sex-reversal. Of these most of the sex-reversal-♀ die. (See later.) By backcrossing the same F₁ ♀ (Tok × Hok) with a third known race we replace in the resulting would-be sons one of the M of the fore-mentioned combination by the M of this third race. If this be the race A this substitution-experiment runs the following way: F₁ ♀ (Tok × Hok) [F_{Tok} M_{Hok}] × ♂¹ race A (F_AM_AM_A) = ♀ F_{Tok} M_A + ♂¹ F_{Tok} M_{Hok} M_A. The females are all normal because the maternal line (the F) which comes from Tokyo, is strong. What are the males? It is evident that in case our analysis is correct, the result depends entirely upon the strength of our Race A. If M_A is a little stronger than M_{Hok} the MM individuals must be high grade intersexual males instead of sex-

reversal females. If we substitute now an M from a race still a little stronger the resulting MM individuals must be males of lower intersexuality than before. Continuing this substitution with M of other races of increasing strength intersexuality of the resulting sons must decrease until with a given strength of the substituted M only normal sons are produced. The results of such a substitution experiment must be in harmony with all other experiments from which an evaluation of the respective strength of the different races is derived. Among the many experiments of this type which have been carried out again and again every single one gave the expected result.

These experiments can and have been varied in different ways, each one being a check on the other. For example, we may start from the combination $F_{Tok} M_{Hok} M_{Hok}$ and leave the two M_{Hok} but substitute another F from a different race, say F_A . Then with decreasing strength of the substituted F the degree of intersexuality of the MM individuals must also decrease. A parallel series may be built up with other M, for example $M_{Hok} M_A$ or $M_A M_A$ or $M_A M_B$. Again a parallel shifting of the degree of intersexuality is to be expected. A large number of such experiments gave invariably the expected, consistent results.

It is evident that it would be possible theoretically to calculate from such a series relative values for the strength of F and M of the different races. In fact this cannot be done. There is a certain amount of fluctuation among the MM individuals which is measured by a classification which cannot be made mathematically exact. At both ends of the series the fluctuation transgresses into the normal (low grade intersexes into normal maleness, high grade intersexes into normal femaleness). But there is no possibility of distinguishing more or less

male males or more or less female females. These facts prevent a calculation of sufficient exactitude.

b. The tests by complex crosses. These tests control not only the relative strength of the different F and M but simultaneously test most decisively the maternal inheritance of F and the situation of M within the X-chromosomes. In these experiments we make crosses involving more than two different races. There is no limit to the complexity of these crosses or the races involved. If sex is controlled only by the relation of F:M, if further these sex-genes are inherited as indicated and if the relative strength of the races involved is known from previous experiments the result of any combination can be predicted. Let us take an example. Let A, B, C, D, E, G be six different races. We cross $A \text{ } \varnothing \times B \text{ } \sigma$, breed from this F_2 , written $(A \times B)^2$; cross an $F_2 \text{ } \varnothing$ to a male, which is an F_1 hybrid between C and D, that is $(A \times B)^2 \times (C \times D)$; a daughter from this combination is crossed to a male which is an F_2 hybrid from $A \times E$, i.e.

$$\left[(A \times B)^2 \times (C \times D) \right] \times (A \times E)^2$$

and finally cross a daughter from this combination to a pure male of the race G. The resulting complex cross is then

$$\left[\left[(A \times B)^2 \times (C \times D) \right] \times (A \times E)^2 \right] \times G$$

If our analysis is correct, the resulting daughters are expected to be the same as if only the cross $A \text{ } \varnothing \times G \text{ } \sigma$ had been made. The maternal line in which the gene F is inherited is derived from the race A, all offspring of this complex cross therefore must have the F_A . The X-Chromosome of a daughter is derived from her father, therefore all daughters of this cross must be $F_A M_G$. If A is a weak race and G a strong one, all these

daughters are intersexual of the same type as the simple cross $A \times G$. Generally speaking, the daughters must be what they are in the simple cross $A \times G$, according to the relative strength of these two races. A very large number of such crosses in the most diversified combinations have been made and invariably they came out according to expectation. As a matter of fact, we have used these complex combinations for many years to keep lines of a definite F , in cases where the pure race is sensitive to inbreeding and dies out after a few generations. The respective gene F of these races is kept in stock by making any crosses whatsoever in the maternal line of the race, provided they also produce normal daughters.

What are the expectations for the sons of such a complex cross? If the maternal line—the first symbol in a formula of the type as above—is weak, only normal males are expected and are in fact bred. If, however, the maternal line belongs to a strong race intersexual males may appear if the proper FMM combinations are possible. In this case an extremely decisive test can be made, as will be shown by an actual example. The following complex cross has been built up among many similar ones:

$$\left[(Ao \times Hok)^2 \times Span \right] \varphi \times \left[(Ao \times Hok)^2 \times \left[\left[(Tess \times Hok) \times (Kum \times Gif) \right] \times \left[(Tess \times Hok) \times Ao \right] \right] \right] \sigma$$

Ao is the very strong race from Aomori; Hok , the very weak race from Hokkaido; $Span$, the very weak race from Spain; $Tess$, the half weak race from the Tessin valley (Switzerland); Kum , the neutral race from Kumamoto; and Gif , another

strong race from Gifu, different in strength from Ao . Thus in this combination six different races representing as many different grades of strength are combined in the complex way indicated by the formula. Seventy-seven sisters of the three-race combination in the left bracket were mated to 77 brothers of the five race combination in the right bracket. The maternal line (the great grandmother of these sisters) belongs to the very strong race $Aomori$ and therefore all offspring must have the strong F_{Ao} , which permits only normal daughters but makes possible the production of intersexual males. According to expectation the result regarding the males depends entirely upon the F and the two M , i.e., the two X-chromosomes, one of which is derived from the mother and one from the father. The sisters used in this cross received their own X from the Spanish father and therefore all sons of the complex cross must have the constitution $F_{Ao} M_{Span} M_X$. What are the expectations for the second M_X ? From the racial constitution of the five race fathers used in our cross, it can easily be derived that theoretically these males might have the following 16 combinations of their two $M(X)$.

- | | |
|--------------|----------------|
| 1. $Ao\ Hok$ | 9. $Hok\ Hok$ |
| 2. $Ao\ Kum$ | 10. $Hok\ Kum$ |
| 3. $Ao\ Ao$ | 11. $Hok\ Ao$ |
| 4. $Ao\ Kum$ | 12. $Hok\ Kum$ |
| 5. $Ao\ Hok$ | 13. $Hok\ Hok$ |
| 6. $Ao\ Gif$ | 14. $Hok\ Gif$ |
| 7. $Ao\ Ao$ | 15. $Hok\ Ao$ |
| 8. $Ao\ Gif$ | 16. $Hok\ Gif$ |

But whereas these males were all brothers, i.e., sons of one father and one mother, their parents and grandparents of course also were always a single pair [no mass cultures], and whereas from a single mating of a female M_K with a male $M_A M_A$ or $M_A M_B$ or $M_B M_C$ never more than two MM combinations can be derived, the result of our cross of the 77

sisters to 77 unrelated brothers can be at most only the production of two types of sons. Which type appears, depends upon the unknown constitution of the fathers, mothers, grandfathers, etc. of these males in regard to their X-chromosomes. But whatever the result, a simple analysis shows that the two types which might appear cannot be any two combinations of the 16 possible male types with the maternal F_{Ao} M_{Span} but only two definite ones belonging together, namely, those produced by males 1 and 2, 3 and 4, 5 and 6 etc. respectively. The 16 types of males then might produce with the M_{Span} of the mothers the following 16 XX or MM combinations among the sons of our complex cross. The phenotypical appearance of these male combinations follows from our previous knowledge of the relative strength of the races. And within one fraternity as in our experiment, only two combinations are allowed to appear and in addition only two belonging together namely, 1 and 2, 3 and 4, etc. The following are the possibilities:

	MM (XX) COMBINATIONS	EXPECTATION FOR ENTIRE OFFSPRING
1	$\frac{1}{2}$ Span Ao $\frac{1}{2}$ Span Hok	3 ♀ : 1 ♂*
2	$\frac{1}{2}$ Span Ao $\frac{1}{2}$ Span Kum	2 ♀ : 1 + ♂ : 1 - ♂ J
3	$\frac{1}{2}$ Span Ao $\frac{1}{2}$ Span Ao	normal sexes
4	$\frac{1}{2}$ Span Ao $\frac{1}{2}$ Span Kum	like Nr. 2
5	$\frac{1}{2}$ Span Ao $\frac{1}{2}$ Span Hok	3 ♀ : 1 ♂*
6	$\frac{1}{2}$ Span Ao $\frac{1}{2}$ Span Gif	normal sexes
7	$\frac{1}{2}$ Span Ao $\frac{1}{2}$ Span Ao	normal sexes
8	$\frac{1}{2}$ Span Ao $\frac{1}{2}$ Span Gif	normal sexes
9	$\frac{1}{2}$ Span Hok $\frac{1}{2}$ Span Hok	only ♀
10	$\frac{1}{2}$ Span Hok $\frac{1}{2}$ Span Kum	3 ♀ : 1 ♂ + ♂ J*
11	$\frac{1}{2}$ Span Hok $\frac{1}{2}$ Span Ao	3 ♀ : 1 ♂*
12	$\frac{1}{2}$ Span Hok $\frac{1}{2}$ Span Kum	like Nr. 10
13	$\frac{1}{2}$ Span Hok $\frac{1}{2}$ Span Hok	only ♀
14	$\frac{1}{2}$ Span Hok $\frac{1}{2}$ Span Gif	3 ♀ : 1 ♂*
15	$\frac{1}{2}$ Span Hok $\frac{1}{2}$ Span Ao	3 ♀ : 1 ♂*
16	$\frac{1}{2}$ Span Hok $\frac{1}{2}$ Span Gif	3 ♀ : 1 ♂*

* In fact 2 ♀ : 1 ♂ on account of the inviability of the sex-reversal-females, see later.

I recall that F_{Ao} M_{Hok} M_{Span} and F_{Ao} M_{Hok} M_{Hok} are sex-reversal = ♀♀, F_{Ao} M_{Span} M_{Kum} male intersexes with fluctuation into normal males, and F_{Ao} M_{Span} M_{Ao} or Gif normal males. The actual result was: 39 cultures with normal sexes and 38 cultures with females, males and intersexual males of the F_{Ao} M_{Span} M_{Kum} type i.e. combinations 3 and 4, altogether about 3400 individuals. I dare any of the critics of our general views, who indulge in general utterances of liking or disliking or possibly modifying factors without trying to analyze the experimental results, to explain this and many other experiments of this type in concrete genetic terms, different from our own.

SEX-REVERSAL MALES AND FEMALES

It is desirable to offer proof that the sex-reversal ♀♀ and ♂♂ which form the ends of the two intersexual series have the gametic constitution of their original sex.

1. Sex-reversal-♂♂ (see 28). A considerable percentage of sex-reversal-♂♂ have been found fertile so that their genetic constitution expected to be XY can be tested. As they cannot be distinguished from ordinary males (for exceptions see the original papers) the only procedure is to mate every single son of a cross weak ♀ × strong ♂, producing only sons, to a female of known constitution. Of the many tests carried out with positive results the following is the most conclusive: We use the females of an F_1 combination Tokyo ♀ × Berlin ♂. Their genetic constitution is F_{Tok} M_{Berl} , Tokyo being a strong race and Berlin a weak one. These females we cross to all brothers from the combination Hokkaido ♀ × Tokyo ♂, giving only males in F_1 . If there are sex-reversal-males of XY—constitution among these, our test crosses must consist of two types:

1. F_{Tok} M_{Berl} ♀ × genuine ♂ M_{Hok} M
2. F_{Tok} M_{Berl} ♀ × reversal ♂ M_{To}

The first combination gives (disregarding the always normal ♀ in the strong maternal line): $\frac{1}{2}$ ♂ $F_{Tok} M_{Berl} M_{Hok}$, $\frac{1}{2}$ ♂ $F_{Tok} M_{Berl} M_{Tok}$. We know from former experiments that a male $F_{Tok} M_{Berl} M_{Tok}$ is a normal male but that an individual $F_{Tok} M_{Berl} M_{Hok}$ is a high-grade intersexual male. The combination 1 therefore must yield normal females, normal ♂ and high-grade intersexual ♂ (of these less than half on account of their inviability). The cross No. 2 however produces only males $F_{Tok} M_{Berl} M_{Tok}$ i.e., normal ♂ besides YY individuals which are expected to be non-viable. The expectation is here therefore 2 ♀ : 1 ♂ and no chance whatsoever for intersexual males. The actual result of such a combination was, when 48 males from an only-male-cross were tested: 29 cultures gave ♀, ♂ and high grade intersexes of the known type, 19 cultures gave only normal sexes, the ratio being 1.8 ± 0.052 ♀ : 1 ♂. This experiment and others of a similar type prove the XY condition of the sex-reversal-males.

2. *The sex-reversal-females* (see 31, 32, 35, 40). Unfortunately the situation for these is different. Hundreds of females of all female cultures, which have been tested in proper experiments, proved to be normal XY females. It was, however, shown that contrary to the behavior of intersexual females, which have a rather high degree of viability, the viability of intersexual males decreases rapidly with increasing intersexuality, the highest types being viable only in a very small percentage. This is still more the case with sex-reversal females, only three having been found altogether, which could be recognized morphologically but which were sterile. Under these circumstances a test for sex-reversal-females corresponding to the one for sex-reversal-males could not be carried out. A probable explanation

for the different behavior of sex-reversal ♀ and ♂ is furnished if the inheritance of F within the Y-chromosome is taken into account.

MODIFYING GENES

It has been mentioned before that in F_2 of the type (strong ♀ × weak ♂)² one-half intersexual males are expected, but that this ratio is not always found. Most frequently only about 1/8 intersexual males appear. In analyzing these cases it was found that in strong Japanese versus weak European races, besides the differences in regard to F and M, a pair of autosomal allelomorphic modifying factors is involved, which affects the expression of male intersexuality (see 20, 40, 53, 56-58). These allelomorphs Tt recombine in F_2 with the MM in simple Mendelian way, thus showing their situation within an autosome. The individuals $M_{weak} M_{weak}$, i.e. half of the F_2 males, ought to be intersexual, but the dominant gene TT prevents this, thus leaving only the tt combinations (1/4 of the $M_{weak} M_{weak}$ males and therefore 1/8 of all males) to become intersexual. [In a certain race combination, which was studied by Lenz, even two such modifying genes were probably present.] The expectations for further generations of such crosses, especially the isolation of pure tt combinations with $M_{weak} M_{weak}$ giving 100 per cent intersexual males, were fulfilled (56-58). Though every detail concerning the action of these modifiers in different combinations is not yet clear, the general facts, as reported, are proven. A parallel case in *Drosophila* is known from Sturtevant's work.

It might be useful to discuss briefly the existence of such modifiers, because misconceptions in regard to the meaning of modifying factors are widespread in genetic literature and lead to still

worse conceptions regarding sex-determination. The action of every gene is normally matched and in tune with the whole genetic system of the developing organism. Otherwise no typical result would be possible. Each mutation in one gene may upset this whole system, provided that the mutated gene acts on a more or less early developmental process. In such a case, therefore, any mutation of a gene might interfere with the action of any other gene. In other words, any mutated gene might act as a modifier to any other gene in action. If we express this more physiologically we may say that a mutated gene might change the internal environment so that the effect of any other gene is consequently modified. Physiologically, of course not genetically, a modification of the internal environment (whatever this may mean in a definite case) brought about by the action of external stimuli is identical with a corresponding change brought about by a mutated gene. It is exactly such a situation which we meet in regard to sexuality. Sexuality (viz. intersexuality) may be shifted by action of external influences within normal genetic constitution (see later). Sexuality or intersexuality may also be shifted by the action of a modifying gene. We may sooner or later find any number of such modifiers, acting in the female as well as in the male direction, of which as many might exist as mutating genes occur. Superficial reasoning will lead then to the conclusion that sex here is determined not by the $\frac{F}{M}$ balance but by the action of these modifiers pulling towards femaleness and maleness respectively. If such a conclusion were possible, the same reasoning would have to be applied to the action of every gene. In other words, there would be no possibility

of connecting any gene with a definite effect. This connection, however, is unavoidable in genetic analysis, though the unspoken addition is to be kept in mind that such a connection applies only to a definite genetic system (containing all the other genes and the specific plasmatic basis) and is changed with almost each gene-mutation or with change of external conditions capable of influencing the system in which the gene acts. Obviously, therefore, the discovery of modifying genes influencing sexual expression has nothing to do with the primary sex-determining agency, the $\frac{F}{M}$ balance, demonstrated conclusively in our experiments.

THE MATERNAL INHERITANCE OF F

The maternal inheritance of F in the gipsy moth is a hundred-fold tested experimental fact (17, 20, 25, 28, 40, 42, 53). Cytologically it might mean that F is either inherited in the protoplasm or in the Y-chromosome. As early as 1912 I pointed out the possibility of F being situated within the Y-chromosome. When the maternal inheritance of F was later established I was constantly looking for a chance to decide this point. This possibility seemed to be given in a genetical analysis of the exceptional females which occasionally occur in all-male combinations. Of all explanations of their origin only one fitted the facts, namely that they are caused by non-disjunction of the sex-chromosomes. If this was the case certain genetical consequences had to follow and all tests which could be carried out agreed with the expectations (20, 27). It was, therefore, concluded that F is most probably inherited within the Y-chromosome; this being, by the way the first case in which the situation of a definite gene

within the Y-chromosome could be made probable by genetic tests. However I never claimed more than probability for this case, first because an absolutely decisive proof could not be obtained and second because one of the consequences was rather shocking, namely that F in the male must have finished its action already before maturation-division, which eliminates the Y in the male eggs.

We are now confident that this final proof will soon be forthcoming. We have found a new genetic test of great value, which also makes possible a cytological control. Experiments are under way. Another chance is given by a recent discovery of Kosminsky (52). He found within normal weak races in Russia lines which regularly throw male intersexes, just as if the F were a strong F. I have suggested that his interesting experiments might be explained by a certain abnormality of the X-Y mechanism. If further experiments prove the correctness of my suggestion a decisive and final test for the inheritance of F within the Y-chromosome will be furnished. We are confident that within the next few years this point will be finally settled.

MORPHOLOGICAL ANALYSIS OF INTERSEXUALITY

At first sight intersexes appear macroscopically as definite stages between the sexes. Closer inspection reveals that the respective stage is the consequence of the amount of admixture of structures of the other sex with the gametic sex. Different organs, however, behave differently according to some law. This was found when it was realized that the intersexual transformation of each organ is reciprocal to the order of differentiation of the organs in development. This fact led to the conclusion that an intersex is developed up to a certain point with the gametic

sex (XX or XY), and from this point on, the turning point, differentiation occurs under the control of the other sex. The degree of intersexuality is, therefore, a direct function of the situation of the turning point in development. This conclusion had to be tested in two ways. First it had to be shown that the increasing series of intersexuality consists for each organ in the addition of a series of developmental stages of the organ with the other sex to the basis of the organ with the original sex. Extended morphological studies for each organ with sexual differentiation made by me and my collaborators (Poppelbaum, Minami, Saguchi, Du Bois) have proven this point. Some additional facts have been discovered by Kosminsky. As a description of all morphological details would require too great space and much illustration, we refer the reader to the original publications, where some of the difficulties in the details are also discussed (17, 20, 23, 25, 26, 29, 31, 35, 46, 50, 51, 54, 55). Though not every single point is completely cleared, the positive evidence is overwhelming. As a matter of fact the analysis is in perfect agreement with the result of the investigation of other cases of intersexuality; viz. the case of *Bonellia*, as studied by Baltzer previous to our analysis, the case of triploid intersexuality in moths, as analyzed by myself (30, 37, 44), and recently the case of triploid intersexuality in *Drosophila* studied by Bridges and Dobzhansky (8).

The second method of attack is the study of the development of different organs in intersexes. An absolutely positive answer has been found in our study of the sex-reversal of ovary and testes in the development of intersexual females and males, where every stage of the transformation of an ovary into a testis and vice versa has been followed (35, 46). Not yet com-

pletely clear are the facts regarding the antennae, where some points of difference in detail exist between Kosminsky and myself (25, 28, 50). Positive again are the results of my student Miss Du Bois regarding the complicated copulatory organ, and Miss Du Bois is now busy filling the last gaps. Altogether the morphological and embryological explanation of intersexuality is safely established.

CONNECTION BETWEEN GENETIC AND MORPHOLOGICAL ANALYSIS

If we put together the genetic and the morphological results, the following situation is safely established: The genetic basis of sex and intersexuality is given by the amount of balance or unbalance between F and M at the beginning of development. The effect of this genic situation is that at a certain moment in development the turning point occurs, that the control of sexual differentiation is shifted from the F to the M genes or vice versa. And the time of occurrence of this event is a simple function of the relative degree of balance or unbalance of $\frac{F}{M}$. These three sets of facts in our opinion cannot be coördinated except under the view that F and M respectively are responsible for a sex-determining or sex-controlling reaction, both of which proceed with a definite velocity proportional to the "strength" or "valency" or, as we see it, quantity, of these genes; that the quicker reaction controls the alternative of sexual differentiation; and that the two curves of the F and M reactions may have points of intersection at a given moment, the turning point, if the quantities of F and M are not properly matched. This inevitable conclusion we have represented in the form of graphs, which are amply discussed in our papers (since No. 17, see 28) and which have been already

discussed in this journal in Crew's articles on sex. We refrain, therefore, from further details.

This physiological solution of the whole problem could be tested by trying to change the relative velocities of these two reactions within a pure normal race by the differential action of temperature. An experiment of this type was already performed in 1909 by Kosminsky, (47) before anything was known of intersexuality. This author as well as myself have since extended these experiments with positive results, producing intersexuality by action of extreme temperature within a pure race (9, 24, 28, 48, 49). Further work on these lines is in progress.

THE X-CHROMOSOME MECHANISM

The analysis of intersexuality has furnished a simple explanation for the two X- one X-mechanism of sex-chromosomes (see 21). This mechanism proves to be an ideal method of securing that of two simultaneous and competing reactions, the F and M reactions, one or the other obtains the higher speed and therewith control of differentiation. The mechanism acts by matching the constant F reaction (maternally inherited F in the gipsy moth, homozygous FF otherwise, M instead of F in the *Drosophila* type) with one produced either by one or by two M (F in the *Drosophila* type), that is, in case of velocities proportional to the quantities, with a slower or speedier M-reaction.

VALENCY OR QUANTITY OF SEX-GENES

We have identified the different valencies or strength of the sex-genes, which are experimental facts, whatever term of description we choose, with their absolute quantities, a conclusion to which many geneticists are vehemently opposed, though no one has tried to make a better

suggestion (vague talk about stereoisomery or polymerisation does not lead to any improvement). It cannot be denied, that a mathematical proof for our conclusion is impossible, so long as a gene cannot be weighed or the numbers of its molecules calculated and conclusions can only be based on definite orderly behavior in regard to the effect of the gene. Agnosticism, is, therefore, an irreproachable attitude. Some people, however, are not content with agnosticism and cannot help trying to formulate theories. The value of such theories is not to be judged by declarations ex cathedra like "neither sound genetics nor sound physiology" but by the recognized demands on any theory in science. In the present case we believe we have shown that we cannot get away from a theory of a quantitative type, that other possible theories entail more difficulties and that our theory, though not the only possible one, is the one which accounts most simply for the thoroughly orderly and consistent series of experimental facts. I am of course the first to accept a better theory, but I am not ready to acknowledge the value of vague and non-committal phrases. The whole question has been recently discussed in No. 42.

THE THEORY OF PLUS-MINUS-MODIFIERS

Though no other explanation for the results of our work has thus far been presented, a modification of our concept has been used by *Bridges* (4-7) in his analysis of triploid intersexuality. There can be no doubt that our analysis of diploid intersexuality can as well be applied to the facts of triploid intersexuality. As a matter of fact, the discoverer of triploid intersexuality, *Standfuss*, has already done this (60, 61) and we have repeatedly shown the same (30, 33, 37). But how about applying the conceptions of *Bridges*

to the case of diploid intersexuality, which must be possible if that conception has any merits? *Bridges* agrees with us that genetically sex and intersexuality are controlled by a balance or unbalance between female and male determiners. But as in triploids this balance finds its visible expression in the relative numbers of autosomes and X-chromosomes and as definite genes could be located in the autosomes, which influence sexual differentiation (modifiers), he preferred to replace the notion of $\frac{F}{M}$ of definite valency

or quantity by a number of plus or minus modifiers, pulling sex towards the female or male side. We have exposed already the error which is made, if from the genetic proof of modifiers for sex a conclusion is drawn on the primary mode of sex-determination. In the triploid *Drosophila*-case it is proven that the X-chromosomes contain F genes (*Drosophila* type of male heterogamecy) without any possibility of claiming more than one such gene if one keeps within the experimental evidence. It is further proven that the M effect is produced by genes in the autosomes, which increase their effect by doubling their number, nothing however being known as to whether they constitute a single pair of allelomorphs or not; and further it is known, that modifying genes exist, probably for pulling sex in either direction. To dissolve the F and M genes into numbers of plus and minus modifiers finds no basis in the experimental evidence, except when basing the conclusions on the forementioned error. But as there can be no doubt any more after the morphological work of *Dobzhansky* and *Bridges* in *Drosophila*, following our analysis of triploid intersexuality in moths, that the phenomenon of intersexuality is identical in diploid and triploid intersexuality, the plus and minus modifier idea ought to

work as well in our case and eventually form an improvement over our analysis. If we try such an application, it is at once clear that in diploid intersexuality, where everything occurs within the normal chromosome set and where the genetic behavior of the things called F and M is completely known, the plus and minus modifier idea can only mean that what appears in heredity as single genes F and M is in fact a completely linked group of plus and minus modifiers; further that what we called the different strength or quantity of these genes is in fact the combined strength or additive effect of different numbers of these modifiers. In other words, everything is as it was, except for replacing a definite number of gene-molecules by a definite number of completely linked genes. What advantage can be gained by such procedure, but to save genetics from such a heresy as the idea that a gene is composed of a definite number of molecules? I cannot help therefore regarding

the plus-minus modifier idea as a minus modification.

GENERALISATION

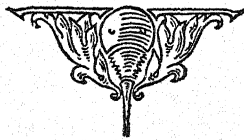
The general theory of sex-determination derived from the analysis of intersexuality in the gipsy-moth has been applied by me and many biologists who accepted my views to the animal and plant kingdoms generally, including also types where the zygotic sex-determination is obscured by the addition of the action of sex-hormones (see 11, 15, 16, 18, 21, 34, 36, 37, 38, 39). These generalisations, which seem to me convincing, in spite of many details waiting for further analysis, and which are being accepted by a steadily increasing number of biologists, are found in a larger set of publications, which have been partly reviewed already by Crew in this journal and have inspired the discussion in a number of modern books and reviews of the problem of sex, i.e., by Crew, Bonnier, Hartmann, Weissenberg, Witschi, etc.

LIST OF LITERATURE

- (1) DU BOIS, A. M. 1929. Morphologische Untersuchungen über die Variationen und die Abnormalitäten des Kopulationsapparates intersexueller Weibchen von *Lymantria dispar* L. Zeitschr. f. Morphologie u. Oekologie, 15.
- (2) BRAKE, B. 1907. Resultate der Kreuzungen zwischen *Lymantria Japonica* Motsch und *L. dispar*. Entomologische Ztschr.
- (3) ———. 1908/10. Continuation of (2). *Ibid.*
- (4) BRIDGES, C. B. 1921. Triploid intersexes in *Drosophila melanogaster*. Science, 54.
- (5) ———. 1922. The origin of variations in sexual and sex-limited characters. Amer. Natur., 56.
- (6) ———. 1925. Sex in relation to chromosomes and genes. Amer. Natur., 59.
- (7) ———. 1925. Haploidy in *Drosophila melanogaster*. Proc. Nat. Ac. Sci. (U. S. A.), 11.
- (8) DOBZHANSKY, TH., and C. B. BRIDGES. 1928. The reproductive system of triploid intersexes in *Drosophila melanogaster*. Amer. Natur., 62.
- (9) EMELJANOFF, N. 1924. Intersexualität bei *Lymantria dispar* unter Einwirkung der Temperatur. Biol. Zentralbl., 44.
- (10) GOLDSCHMIDT, R. 1911. Die Vererbung der sekundären Geschlechtscharaktere. Mitt. Ges. Morph. u. Phys. München, Nr. 49, (Sitzg. v. 21. Nov.).
- (11) ———. 1912. Erblichkeitsstudien an Schmetterlingen I. Zeitschr. f. ind. Abstammungslehre, 7.
- (12) ———. 1913. Weitere Untersuchungen über Vererbung und Bestimmung des Geschlechts. Mittlg. Ges. Morph. u. Phys. München, Nr. 30. (Sitzg. v. 8. Juli).
- (13) ———. 1915. Vorläufige Mitteilung über weitere Versuche zur Vererbung und Bestimmung des Geschlechts. Biol. Zentralbl., 35.
- (14) ———. 1916. A preliminary report on further experiments in inheritance and determination of sex. Proc. Nat. Ac. Sci. (U. S. A.), 2.
- (15) ———. 1916. Experimental intersexuality and the sex-problem. Am. Natur., 50.
- (16) ———. 1916. Die biologischen Grundlagen

- der konträren Sexualität und des Hermaphroditismus beim Menschen. Arch. Rassen- u. Ges. Biol., 12.
- (17) GOLDSCHMIDT, R. 1917. A further contribution to the theory of sex. Journ. Exp. Zool., 22.
- (18) ———. 1917. Intersexuality and the endocrine aspect of sex. Endocrinology, 1.
- (19) ———. 1919. Intersexualität und Geschlechtsbestimmung. Biol. Zentralbl., 39.
- (20) ———. 1920. Untersuchungen über Intersexualität. Ztschr. f. indukt. Abstammungsl., 23.
- (21) ———. 1920. Mechanismus und Physiologie der Geschlechtsbestimmung. Berlin, Bornträger (Engl. Ed. Methuen Co. 1923).
- (22) ———. 1921. Erblichkeitsstudien an Schmetterlingen III. Der Melanismus der Nonne *Lymantria monacha* L. Zeitschr. ind. Abstammungsl., 25.
- (23) ———. 1921. Analyse der Doppelmissbildungen. Arch. Entwicklungsmech., 47.
- (24) ———. 1921. Zur Entwicklungsphysiologie der Intersexualität. Naturwissenschaften, 9.
- (25) ———. 1922. Untersuchungen über Intersexualität II. Zeitschr. f. ind. Abstammungsl., 29.
- (26) ———. 1922. Die Reifeteilungen der Spermatozyten in den Gonaden intersexueller Weibchen des Schwammspinner. Biol. Zentralbl., 42.
- (27) ———. 1922. Ueber Vererbung im Y-Chromosom. *Ibid.*, 42.
- (28) ———. 1923. Untersuchungen über Intersexualität III. Ztschr. induktive Abstammungsl., 31.
- (29) ———. 1923. Einige Materialien zur Theorie der abgestimmten Reaktionsgeschwindigkeiten. Arch. mikrosk. Anatom., 98.
- (30) ———. 1925. Bemerkungen über triploide Intersexe. Biol. Zentralblatt, 45.
- (31) ———. 1925. Ueber die Erzeugung der höheren Stufen der männlichen Intersexualität bei *Lymantria dispar*. *Ibid.*, 45.
- (32) ———. 1926. Nachweis der homogametischen Beschaffenheit der Geschlechts umwandlungsweibchen. Biol. Zentralbl., 46.
- (33) ———. 1926. The quantitative theory of sex. Science, 64.
- (34) ———. 1926. Bemerkungen zum Problem der Geschlechtsbestimmung bei *Bonellia*. Biol. Zentralbl., 46.
- (35) ———. 1927. Weitere morphologische Untersuchungen zum Intersexualitätsproblem. Zeitschr. f. Morph. u. Oekol., 8.
- (36) ———. 1927. Zygotische Geschlechtsbestimmung und Sexualhormone. Naturwissenschaften, Jahrg. 15.
- (37) GOLDSCHMIDT, R. 1927. Die zygotischen sexuellen Zwischenstufen und die Theorie der Geschlechtsbestimmung. Ergebnisse d. Biologie, 2.
- (38) ———. 1928. Die Theorie der Geschlechtsbestimmung, Scientia, März.
- (39) ———. 1929. Geschlechtsbestimmung im Tier- und Pflanzenreich. Biol. Zentralbl., 49.
- (40) ———. 1929. Untersuchungen über Intersexualität IV. Zeitschr. f. indukt. Abstammungsl., 49.
- (41) ———. 1929. Untersuchung zur Genetik der geographischen Variation II. Archiv. Entwicklungsmech., 116, I.
- (42) ———. 1930. Untersuchungen über Intersexualität, V. Zeitschr. f. indukt. Abstammungslehre, im Druck.
- (43) ———. u. S. MINAMI. 1923. Ueber die Vererbung der sekundären Geschlechtscharaktere, Studia Mendeliana.
- (44) ———. u. K. PARISER. 1923. Triploide Intersexe bei Schmetterlingen. Biolog. Zentralbl., 43.
- (45) ———. u. H. POPPELBAUM. 1924. Erblichkeitsstudien an Schmetterlingen II. Zeitschr. indukt. Abstammungslehre, 11.
- (46) ———. u. S. SAGUCHI. 1922. Die Umwandlung des Eierstocks in einen Hoden beim intersexuellen Schwammspinner. Zeitschr. f. d. ges. Anat., Abtlg. 3: Ergeb. d. Anat. u. Entwicklungsgesch., 65.
- (47) KOSMINSKY, P. 1909. Einwirkung äusserer Einflüsse auf Schmetterlinge. Zool. Jahrb., Abtlg. Syst., 27.
- (48) ———. 1924. Ueber Erzeugung von Intersexen bei *Stilpnotia Salicis* L. im Temperatur-Experiment. Biol. Zentralbl., 44.
- (49) ———. 1924. Der Gynandromorphismus bei *Lymantria dispar* L. unter der Einwirkung äusserer Einflüsse. Biol. Zentralbl., 44.
- (50) ———. 1929. Die Entwicklung der Antennen bei intersexuellen Weibchen des Schwamspinner (*Lymantria dispar* L.), die durch Bastardierung verschiedener Rassen erhalten werden. Biol. Zentralbl., 49.
- (51) ———. u. X. GOLOWINSKAJA. 1929. Zur Morphologie des Geschlechtapparates der Lepidopteren. Ztschr. f. Morph. u. Oekol., 15.
- (52) ———. u. ———. 1930. Untersuchungen über die sogen. "Scheinzwitter" des Schwamspinner. Zeitschr. f. indukt. Abstammungsl., 53.
- (53) LENZ, F. 1923. Erfahrungen über Erblichkeit

- und Entartung an Schmetterlingen. Arch. Rassen-u. Ges. Biol., 14.
- (54) MINAMI, S. 1925. Untersuchungen über das Flügelmosaik intersexueller Männchen von *Lymantria dispar* L. Arch. mikrosk. Anatomie, 104.
- (55) POPPELBAUM, H. 1914. Studien an gynandromorphen Schmetterlingsbastarden aus der Kreuzung von *Lymantria dispar* L. mit *japonica* Motsch. Zeitschr. ind. Abstammungsl., 11.
- (56) SCHWEITZER, A. 1915. Ueber Kreuzungen zwischen *Lymantria dispar* L. und *L. dispar* var. *japonica* Motsch. Mittlg. d. Entomologia, 1.
- (57) SCHWEITZER, A. 1916. *Idem., Ibid.*, 2.
- (58) ———. 1918. *Idem., Ibid.*, 4.
- (59) SEILER, J. 1914. Das Verhalten der Geschlechtschromosomen bei Lepidopteren. Arch. Zellfg., 13.
- (60) STANDFUSS, M. 1908. Experimentelle zoologische Studien. Denkschr. schweiz. Ges. Naturw.
- (61) ———. 1914. Mitteilungen zur Vererbungsfrage. Mittlg. schweiz. entomolog. Ges., 12.
- (62) ———. 1915. Beiträge zu der Arbeit von Schweitzer, A. 1915: Ueber Kreuzungen zwischen *L. dispar* und *L. dispar* var. *japonica*. Mitt. Entomologia, 1.





BIOLOGICAL ORGANIZATION

By DAVID L. WATSON

Department of Physics, Antioch College

"Ni les recherches spéciales, ni les vues générales, ne suffisent isolément à constituer aucune science: c'est par leur alliance, par leur union, qu'elle se fonde et se développe."—CLAUDE BERNARD.

PHYSICAL concepts have no necessary finality or inevitability. They take rise in response to pragmatic requirements and in harmony with the context of ideas and phenomena prevailing at the time of their birth; they persist in proportion to their success in the symbolic formulation of these and of new experiences. The recent revisal of the foundations of physics required by relativity and the new quantum theory has shown us clearly that as this context changes the concepts themselves change their significance and indeed may lose their original meaning. The physicist is thus faced continuously with the duty of sceptically reviewing his trusted theories and of discounting as far as possible those features of them which can be traced to historical accident. Further, as these new advances have taken him close to the fields of philosophy, psychology, and biology he is bound to recognize that the experiences of these sciences must be understood in each new formulation of his own concepts.

Physics abstracts certain limited features from the richness of direct experience, but no further attention is paid to the other aspects of the total experience from that point on. The assumption is made that these other aspects can be ignored always because they can be ignored in the initial stages. As our knowledge and insight

grow, we may find that the old concepts and symbols are not best adapted to apprehending and summarizing newer phenomena. From time to time aspects of a problem arise which require that we take into consideration unfamiliar kinds of abstraction. Any set of abstractions by its very nature places a fatal limitation on the kinds of observations we will make or on the range of problems which it can handle successfully. At the time of Newton, it was not quite clear that the characteristics of matter and space so far discovered (such as extension) were sufficient to account for everything (31). The distortion implicit in physical concepts because of certain vaguenesses about methods of measurement has been demonstrated and corrected by Einstein and Heisenberg (1) and analyzed in detail by Bridgman (3), but other viewpoints of the intuitive Newtonian picture of the world are just as much in need of a constant vigilance and revision. Such considerations have in the past been avoided because they are metaphysical.

The suggestions of the following paper may have value in directing thought in biology and psychology along somewhat new lines. It is true that much thinking in the latter sciences has divorced itself from the bounds imposed by the physicists' view of the world, but there is a large region in both sciences where the rigor of thought and resource in experi-

ment characteristic of physics form the dominant note. The biologists and psychologists engaged in exact investigation are still operating in a mood of exaggerated awe of the methods, concepts, and laws of physics, and they will not be inclined to side with the philosophic followers of their own sciences if it cannot be shown to them that physics itself will countenance a more tolerant point of view. Hence the necessity of indicating where some of the unsolved problems of biology impinge on physical theory and of endeavoring to modify the physical picture in the light of them. This process reacts favorably on physics itself, for it brings to light some inadequacies of theoretical physics. In particular, I shall attempt to show that the second law of thermodynamics as ordinarily understood does not tell us as much about organic systems as we thought it did.

As an illustration of such an unsolved problem, one might consider the growth curve. In a recent paper, J. Gray (11) concludes that "although it is possible to express the final growth curve by means of a simple formula, this formula cannot throw any real light on the underlying causes of growth." His paper is taken up largely, however, with a discussion of the best differential equation for the curve. This dilemma is typical of those produced by the quantitative, atomistic, differential-calculus, Euclidean ideology of many contemporary biologists and can only be corrected by a more qualitative, configurational or organismal, logico-symbolical, phenomenological viewpoint.

THE MEANING OF PROBABILITY

The concept of probability needs an examination from the above point of view. The arbitrariness inherent in it has been brought to attention recently by the establishment of new statistical

theories in which the calculation of the probability of a state proceeds on different bases from that employed with such success in the classical kinetic theory of gases and in statistical mechanics. The disconcerting nature of probability as a physical concept had been recognized before this development by mathematicians, physicists, and philosophers. If we are to calculate the probability of an event, it is certain that our estimate will depend on the relevant facts at our disposal. If we know all the circumstances which can affect the occurrence of this state or event, the probability can have only one of two possible values: 1 or 0. (This is the case in classical deterministic mechanics.) Intermediate values are possible only because of our ignorance of one or more of the controlling factors.

This is the state of affairs with thermodynamic quantities. "If the atomic picture could be made more definite, the meanings which we . . . attach to entropy and temperature would be dissolved. Our theory of these entities depends upon the vagueness of the picture." (Darrow, 6). The same indefiniteness is to be found in the new quantum theory. "The new mechanics knows no exact initial conditions. The classical alternative—either necessary or impossible—it does not know. For it, *anything* is to be regarded as possible. Correspondingly, the new mechanics does not concern itself with the discovery of certain events having a given probability, but with the study of *the probability of all possible events*." (Condon, 5). The latter admission is of intense interest for the Gestalt considerations of the last section of this paper.

From this point of view, the accepted value of the probability in a given case reflects the state of our knowledge regarding the phenomenon. As Eddington (9)

has said, "Unless it belies its name, probability can be modified in ways which ordinary physical entities would not admit of. There can be no unique probability attached to any event or behavior; we can only speak of 'probability in the light of certain given information,' and the probability alters according to the extent of the information." Further, probability depends on the *assumptions* made or *conventions* used in calculating it, even though the "facts" are agreed on.

Briefly, probability depends on: (1) the facts known, (2) the assumptions used. If I toss a coin ten times and get ten heads, the probability of throwing a head on the next trial depends on the assumptions I am willing to make as to the importance of the knowledge derived from the previous trials, it being assumed that I have no other knowledge about the coin. Now if I were tossing the coin for the first time, I should take the probability of head to be one-half, which I should also conclude in this case for the eleventh trial if I act on the assumption that a biased or false coin is essentially impossible. However, if I admit the assumption that the coin may be biased or double-headed, or that the method of throwing may be selective, then the ten successive heads give me a measure of the probability that the coin is defective (Bayes' formula), and the probability of head on the next throw is now greater than one-half. After one hundred throws of head, I should, on the second assumption, be still more certain that the coin was defective and so the probability of a head on the one hundred and first throw would be nearly 1. Thus our estimate of the probability in this case depends on the facts known (the number of previous successive heads) and on the assumptions (allowability of defect, etc.). This aspect of probability is discussed by C. J. Fry (10): "To the Omnis-

cient the answer (of a probability problem) is either unity or zero. It is neither to us, because we are in neither state of knowledge (omniscient or completely ignorant). . . . Probability is a measure of the importance of our state of ignorance, (and) it must change its value whenever we add new knowledge." Or, A. J. Lotka (22): "Probability is essentially a matter of classification. An improbable event is one that is a member of a small class and whether it is so or not depends on our system of classification". . . . "It is meaningless unless the characteristic with regard to which the probability is reckoned is explicitly or implicitly indicated." In the same connection, Reiser (27) decides: "In this view, probable knowledge does not imply contingency or indetermination, but only that our knowledge is insufficient to predict the event. This interpretation seems to render 'chance' subjective."

It is possible that while the conventional classification is most valuable for physics there may be other methods for living systems—which depend for their success on the more immediate accessibility (in organic systems) of other kinds of facts. The suggestions of this paper are based on such a possibility. Other classifications of the possible arrangements, however, are subject to grave difficulties because they do not have the advantages of (1) homogeneity or uniformity throughout all nature, (i.e., they cannot be applied in the same way to all systems: they must be specific or so to say, local); or of (2) quantitative manipulability. The abstractions on which these other classifications are based are qualitative or non-commutative: their most important criterion is morphological or functional. Our common everyday mathematics does not lend itself to the treatment of these. Fortunately, A. J.

Lotka has suggested ways of attacking the problem, and J. H. Woodger has shown the way to the application to it of the method of symbolic logic and related fields. In the words of the latter (39): "It is not so much the mathematical laws of physics that we require but the mathematical *method* in the broadest sense, and this is quite a different thing." (Different from "applying" mathematics to biological data.) We need a "revision of our ways of thinking," and shall have, for this purpose, to explore some little known regions of the "realm of abstract logical entities and relations."

ENTROPY

The entropy concept is related to the probability of a state by the Boltzmann formula:

$$S(\text{entropy}) = k \log(\text{probability}),$$

where k is the gas constant for a single molecule, and we must conclude that the factors which influence the probability—in particular the knowledge or assumptions about the phenomena—will also change the value of the entropy.

The tendency towards increased entropy which we call the second law of thermodynamics was reread by Boltzmann to mean that *a system of itself will change from less probable to more probable states*. This statement gives us at first an agreeable feeling of increased understanding but it is "indefinite in failing to specify with regard to what characteristic probability is to be reckoned." (Lotka, p. 35.) A. J. Lotka has given a very convincing example to show that the apparent improbability of a *rare* event is due to our *method of regarding* the event. A series of 50 cards is numbered 1 to 50 and equally divided between two urns, A and B. A card from A and one from B are interchanged and their numbers noted, this process being re-

peated several times. After any arbitrary number of exchanges, the cards in urn A are painted black on the reverse side and the interchanging continued as before. From this point on, the behavior of the system is conventional; i.e., it changes continuously towards the ("most probable") state of equal distribution of black and white between the two urns ($12\frac{1}{2}$ in each). Before the painting, however, the change is towards the "very improbable" distribution in which all the white cards are in one urn and all the black in another. In other words the "probability" characteristics of a system are imposed on it by ourselves for convenience. A "rare" event is one which we can identify more precisely than a "more probable" one—for the latter has more ways of being realized.

We are thus faced with a very serious kind of absurdity in the second law. If our knowledge of the structure of the world were complete for all times, the probability of one *particular* configuration for each instant would be 1, of all other configurations 0. To say that a system changes from less probable to more probable is merely to say that our assumptions are such that earlier events fall into a class of small frequency (therefore more completely definable) and that later events must be classified with many others from which they cannot be differentiated because our knowledge of them is progressively less able to assign them either to the class of probability 1 (the event which transpires) or of probability 0 (all other possible events). We, for some reason, are generally on the downward slope of Lotka's curve (p. 31). (He plots "number of tickets in urn A after n th draft" as ordinate against n , "the number of double drafts" as abscissa.)

There are two possible reasons for this: (1) The assumptions on which our analy-

sis is based are in some way similar to the conventional type of probability problem—that is, one in which little difference of opinion is possible as to the grouping of possible events. However, we may remember during our own introduction to the calculus of probabilities how easy it was to make an unorthodox interpretation of a problem to obtain a new value of the probability and how by being careless of our hypotheses it was possible to arrive at absurd results—for instance, that there is life on Mars: (10).

(2) The intrinsic nature of *physical processes leads us to prefer this kind of classification* above all others.

Evidently the second law will have a modified significance if we can arrange our apprehension of events in the same way as Lotka does to produce an *upward* trend of the curve (i.e., towards less probable states). Here, however, we are held up until we decide whether or not the physical facts will allow a process analogous to painting half of the cards black, at any arbitrarily chosen instant. We cannot do this if we are interested only in the available energy and arbitrarily name the state of maximum entropy "the most probable." However, if we mean available-in-the-light-of-the-biological-organization-present, or use some other criterion, we *may* transpose the "painting black" to some other point of the process. The peak of the curve (i.e., all black in urn A) will not now appear at the same ordinal number in the series of (double) exchanges and because of the emergence or introduction of organic or psychic wholes in the system may appear later and provide an apparent decrease of "something-corresponding-to-entropy."

By setting aside mechanical work as our criterion, we can perhaps produce a number of peaks (or "least probable" arrangements) dependent on the principle

with regard to which the events are classified (as shown later in this paper from another angle). This is G. N. Lewis' idea when he says of the permutations of four playing cards (ace, two, three, and four of spades): "There is no one of the twenty-four arrangements (other than the 1, 4, 3, 2 of whist) which might not be particularly significant *in some other card game*." Or: "There is no such thing as a well-shuffled pack except with reference to familiar sequences." (21).

G. N. Lewis has succeeded in showing very clearly that for a mixture of three different gases the entropy depends on our knowledge (or "information" he calls it) by using either Maxwell Demon considerations or an arrangement of two pistons with differing semipermeable properties in the manner of the Gibbs paradox problem. His analysis proves clearly that "the increase in entropy comes when a known distribution goes over into an unknown distribution," that "Gain of entropy always means loss of information and nothing more," and, very significantly for later portions of this argument, that "It (entropy) is a *subjective concept*." (21).

These considerations have been forcing themselves on us for some time. Schottky (28) makes a distinction (in which Lewis' analysis is implicit) between what he calls "formal" and "technical" entropies. In conversation with the author on the problem of Gibbs' paradox in July, 1929, K. F. Herzfeld delivered himself of the opinion that "reversibility depends on the criterion of separability" and that entropy does depend on our knowledge: "A state of which little is known embraces a large number of possibilities," he said. The entropy of a state then decreases as our knowledge of it increases and, as we concluded at that time, assumptions and conventions must be taken into account as well as Lewis' "information."

I am told by a mathematical physicist that this indefiniteness does not influence the experimental fact. I would answer (1) These considerations influence our interpretation of the facts, render them less able to mislead us and will certainly lead to unsuspected new facts. (2) The experimenter must report his experiment in words and if we wish to know what has happened we had better be clear as to what he means by these words. Kelvin, Clausius, and Boltzmann were not reporting on experiments when they explained to us the meaning of the second law.

It is true indeed that "the universe is running down," but the amount of available energy which will be *successfully* tapped off for human (or living) purposes is not predetermined alone by the intrinsic energy-properties (i.e., thermodynamics) of materials. The available energy in the world, of which Boltzmann talked so poetically, is, from this point of view, as academic as the total amount of (almost entirely) unavailable energy. In a highly organized system, the "available" energy is a function not only of p , v , t , and the state of chemical combination, but of the nature and degree of organization of the matter present. The practical question is: How much of the available energy will we succeed in using? It might all go to waste or we may use varying amounts of it up to the total amount. This question can be answered only by not ignoring the knowledge available, or the organisms and machines to be used. We cannot, of course, give a quantitative answer except in very simple cases, but we can treat isolated systems with these ideas in mind or, at worst, admit this limitation of the physical analysis.

We shall feel more confident about these apparently unsettling conjectures if we go back to the origin of the first law of thermodynamics. Helmholtz says (16):

Science regards the phenomena of the material world according to two processes of abstraction; in the first place it looks upon them as simple existences, without regard to their action upon our organs of sense or upon each other; in this aspect they are termed *matter*. . . . When we wish to make actual application of our idea of matter, we can only do it by means of a second abstraction and ascribe to it properties which in the first place were excluded from our idea, namely the capability of producing effects, or in other words, of exerting *force* (energy). It is evident that in the application of the ideas of matter and force (energy) to nature the two former should never be separated. . . . Both. . . . are abstractions from the actual performed in precisely similar ways. Matter is only discernible by its forces, and not by itself.

Extending his argument, I would say: Available energy is only "discernible" with the cooperation of mechanisms or organisms "and not by itself." Newton and Galileo successfully worked with the concept of matter in isolation just as physics has up till now successfully separated itself from biology and psychology. Later, to the simple concept of matter in its gross dynamical relationships, Nernst and others have added the further abstraction of "chemical energy." If (quoting Helmholtz again) "we wish to make actual application of our ideas" of matter and energy "we can only do so by means of an abstraction" to which we vaguely refer as organization, life or intelligence, and I would argue for placing these now in the picture that Helmholtz gave us, and that a separation is no longer justified.

MAXWELL'S DEMON AND THE ORGANISM

The possibility that the second law of thermodynamics may not apply to living systems rests mainly on the idea that an organism for some purposes may function in a manner similar to Maxwell's Demon. If we attempt to formulate specifically the function of the latter, for instance, when it divides a mass of gas of homogeneous temperature into two portions of

differing temperature we find the following: (1) the Demon is able to observe certain microscopic features of the system and to base his action on the result of these observations; (2) the outcome of his activity is that the system previously homogeneous with regard to the variable he is observing has now become heterogeneous or differentiated.

We might consider the "purpose" of such a creature to be the setting up of temperature differences. We attach importance to this because in the system thus modified, part of the random heat energy of the molecules has become available for the performance of useful work. From the point of view of the Demon, or regarding this "purpose" alone as a standard to be aimed at, it is reasonable to say that the system in its later states is more highly organized, or, if we have in mind the subsequent application of this organization to performing work outside the system, he might be regarded as having directed some of the uncoordinated motion of the molecules into the coordinated motion, for instance, of the flywheel of an engine. His activities may be summed up by saying that by the selection or choice of favorable events an increase of order or coordination, or a decrease of disorder is made possible.

It is generally believed that this mechanism cannot lead to a reversal of the second law in living matter. Smoluchowsky shows that such an unidirectional opening is not physically possible, either because it is subject to fluctuations itself or because its stability would of itself prevent it from opening. "Eine Gleichrichtung der ungeordneten Molekularbewegung ohne Energieverlust ist auch in beliebig klein dimensionierten Strukturen unmöglich." (Coordination of disordered molecular motion without loss of energy is impossible even in structures of vanishingly small

dimensions.) (25) (29). However, it appears that one of the outstanding characteristics of life shows certain similarities to the above. (This was pointed out by Lotka at a meeting of the Cosmos Club, May 31, 1924.) Life modifies the "organization" of matter in two ways: (1) it breaks down undifferentiated food stuffs and reorganizes them into cells and that arrangement of cellular parts most adapted for the purposes of the organism, that is, self-perpetuation and protection, excitability, nutrition, motion, reproduction, etc. (2) The organism acting as a unit modifies the distribution of matter and of large scale objects in its environment with essentially these same objects in view, as for instance when the bird builds a nest or a man his house. The selection or organizing carried out by the organism is not with respect to velocity as in the case of the Demon, but, for instance, with respect to chemical composition, space-distribution, or configurational properties. Unlike the Demon too the selection of the organism may be macroscopic.

I wish to avoid the suggestion that these considerations involve a possible interference with the second law as ordinarily understood, or that the Demon as a quasi-intelligent agency is necessary for the creation of biological organization.

WHAT IS "ORGANIZATION"?

If you ask what specifically I mean by "organization," the answer might be given that the more highly organized system has more possibility of undergoing a given kind or greater variety of experience. (Evidently two terms are necessary for these distinct cases. We might call them respectively "convergent" and "divergent" organization.) It is thus evident that we cannot separate the conception of degree of organization from

what I have called the "purpose" of the organizing agent; that is, the end-state of the system used as reference. We here use the word "purpose" not implying there is some directing agent, vital principle or entelechy which determines the development of the organization. A system will be said to be organized with reference to a "purpose," r , insofar as it is a step on the way toward complete attainment of the final pattern or process, r . It is this postulated final state which we shall call the "purpose." For a germ cell, the "purpose" might be the standard dynamic arrangement of chemical substances and cells so functionally related as to have the properties of the mature organism which the germ cell will later attain.

Consider two states (or complexions), (1) and (2), of a system. Let r be the "final" state hoped for—or used as reference in the calculation—and let φ_{1r} , φ_{2r} be the respective probabilities (in the light of the knowledge available) of the changes $1 \rightarrow r$ and $2 \rightarrow r$, (φ 's assumed dependent on the nature of the initial state and final state). If $\varphi_{1r} > \varphi_{2r}$, we may regard state (1) as *more highly organized* than state (2) with reference to purpose (r). The measure of organization here suggested implies, then, the imagined completion of a certain type of process, the end-state attained being a standard against which the degree of organization of other states is measured. A state (1) which has a greater degree of organization than another (2) with reference to state (r) has a molecular arrangement in which the transition to (r) is inherently more probable—that is, attainable either by equally probable transitions from a greater number of equally probable complexions or realizable by a greater number of equally probable transitions from one given complexion. With reference to another pos-

tulated end-state (s), however, the probabilities φ_{1s} , φ_{2s} in both cases might be very different.

PROBABILITY OF TRANSITION

This analysis implies a dependence on *probability of transition* about which pure thermodynamics has had little to say. The field of chemical reaction velocities deals empirically with one aspect of this. Raschevsky (26) has suggested on purely physical grounds a general principle in this field:

$$\frac{d\lambda}{dt} = \kappa \frac{\partial S}{\partial \lambda}$$

where λ = the parameter which is changing—pressure, concentration or mass,

S = entropy, and t = time, and κ is a function for a particular type of change. This equation has not yet been experimentally verified or disproved. Lotka (22, p. 357) infers from biological evidence that an isentropic system tends to change so that the total flux of energy through the system is a maximum. The new quantum theory has also begun to handle such problems.

We might, of course, avoid the difficulty by assuming in simple cases that the probability of a transition is independent of the initial state and dependent only on the probability of the final state reached. This, however, is manifestly unsound. The addition of a catalyst alters the probability of a chemical change though the products may remain the same. Such a suggestion, too, ignores the present idea of degree of organization as a measure of intermediate configurations.

G. N. Lewis (21) has brought forward some considerations in this connection which tend to show that the intrinsic probability of transition from one ele-

mentary quantum state to another depends equally on the initial and final states. Indeed, he believes that, as the relationship must be symmetrical, $\varphi_{ab} = \varphi_{ba}$.

NOTE 1. Probability of transition has no obvious connection with probability of a state as ordinarily handled in statistical mechanics. However, it is possible to imagine in special cases that the a priori probability of a given state is a function of the probabilities or frequencies of the various transitions by which it could arise from other configurations whose a priori probabilities are known.

Let $P_1, P_2, \dots, P_r, \dots$ be the a priori probabilities of various states, (1, 2, \dots, r, \dots)

$\varphi_{1r}, \varphi_{2r}, \dots$ the "intrinsic" probabilities of the transitions from each of these states to state r .

Then $P_r = f_1(\varphi_{1r}, P_1) + f_2(\varphi_{2r}, P_2) + f_3(\varphi_{3r}, P_3) + \dots$ where f_1, f_2, f_3, \dots are certain functions to be determined.

These P 's differ from the p 's of Lewis in that the states to which they apply may embrace a number of elementary states or permutations. The present φ 's are subject to the same distinction.

The word purpose as applied to conscious animals generally has metaphysical connotations as to the nature of the force impelling the animal toward attainment of its purpose. We do not wish to imply any such finalism or teleology. In ordinary language "purpose" implies some agency which foresees an end and superimposes its will on a system in the light of this end. Such an agent is regarded as interfering with chance. It is not necessary, however, to hold any belief contrary to the spirit of physics in order to regard the final upshot of a synthetic change as if it were arrived at because of known forces whether in physics, biology, or psychology. The concept of purpose used in this essay means simply the final configuration with reference to which other arrangements are judged. The extent of the preference of a given intermediate system (a) for a given end-state (r) is measured statistically by noting the

number of times the system (a) develops into (r) in relation to the total number of changes. This interpretation of purpose has been discussed recently by Krikorian. "The purpose of act or object (is) the *expected end-result* of that act or object." (18).

Evidently such an interpretation is just as applicable to a purely physical system as to an organic one. The "purpose" of a dynamical system is the state of least potential energy or minimum free energy. Mach (23) says: "We can conceive of the natural forces of attraction or repulsion as purposes or intentions of nature. . . . It is the purpose of nature, accordingly, to bring the iron nearer the magnet, the stone nearer the centre of the earth. . . . If such a purpose can be realized it is carried out." The "purpose" of the Maxwell Demon and his partition, if such could be realized, is a state of lower entropy.

"Organization" is applied either to structure or to the setting up of the structure. We shall use the word in its static sense and the expression "process of organization" for the latter. We must also differentiate between organization which finds its expression in a certain structure or—as in the physical case—in the fact that this structure is instrumental in realizing a certain process—though in biology these are interlinked.

ENTROPY AS A MEASURE OF ORDER

In measuring organization we must surely bring to light the tacitly assumed criterion of "organizedness." In physical systems we have, in the past, used the free energy or the entropy as a measure. There the reference end-state is the state of minimum free energy or of maximum entropy, but in both these cases the reference end-result is the state of *least* organization and not, as in my suggestion, the

state which is best adapted to, or most highly organized for, the end in view, (which is, presumably, the conversion of all the available energy into mechanical effect). The physical organization also differs from that suggested earlier in this paper in that it can be measured by the free energy available *if* the system changes to the "disorganized" state, i.e. by the use which *can* be made of the organization once set up (if it is so used) not by the *probability* that such use will *actually* be made (which would be the analogue of our "probability-of-change" criterion). For this reason one might adopt as a measure, instead of the transition probability method, the use of a more "generalized" entropy as defined by the Boltzmann formula $S = k \log_e (\text{probability})$. Here, of course, the probability is the a priori probability of the state or complexion, taking all relevant facts into consideration, and the measure is of "disorder" (36). Professor Herzfeld has suggested to me that we use "order" and "disorder" in physical chemistry and "organization" and "disorganization" where bio-psychophysical concepts are introduced and of which a more "generalized" entropy might give a measure.

The *a priori* probability of a state is defined in physics as (Herzfeld, 14)

- (1) the limiting value of the fraction of the total time of observation for which a specified state is realized when the time is made longer and longer—which, for a large number of observations, is identical with
- (2) the fraction of all the individual random observations for which the system occurs in the desired state or with
- (3) the relevant fraction of the total number of possible arrangements of the system, that is,

$P_1 =$ the ratio

$$\frac{\text{number of individual ways in which this state (1) is realized}}{\text{total number of permutations of the system}}$$

It might be better in view of the discrepancies mentioned above between the physical and methods of calculating the probability and end-state to avoid overstressing the analogy with entropy and define the change in the "*r*-type-disorganization" as

$$\log_e \frac{\text{a priori probability of (1)}}{\text{a priori probability of end-state (r)}} = \log_e \frac{P_1}{P_r} = \log_e P_1 - \log_e P_r$$

The inclusion of the second term emphasizes the fact that entropy difference is the essential quantity. If we use the Boltzmann constant k for convenience (though it has only formal significance here) this quantity might be written

$$\frac{\Delta \sigma_r}{k}$$

or

$$\frac{1}{k} (\text{"r-type entropy" change}).$$

It is assumed here that the reference state is the one of highest organization, i.e., $P_r < P_1$ and $P_r < P_2$. Note however that the definition of "purpose" is such as to admit either less ordered or more ordered as legitimate end-states. This method gives us a scale on which to classify state (1) with reference to the end-state used, as does entropy in physical changes. In physics the entropy change is measured by

$$\Delta S = k \log_e \frac{\text{probability of state (1)}}{\text{probability of state of maximum entropy}} =$$

$$k \log_e \frac{P_1}{P_{\max.}} = k (\log_e P_1 - \log_e P_{\max.})$$

In thermodynamics the denominator of the fraction is often omitted. The more highly ordered state has the smaller entropy and therefore increasing order means decreasing S . Similarly the greater

is σ , the greater is the "disorganization" with reference to (r).

Can this treatment be reconciled with our previous definition of "more highly organized?" The earlier method makes the state of greater " r -organization" that for which the transition to r is more probable. If (1) is "more highly organized" than (2) or $\varphi_{1r} > \varphi_{2r}$ (transition probabilities) we should expect the " r -type entropy change" from $1 \rightarrow r$ to be less than the " r -type entropy change" from $2 \rightarrow r$. That is,

$$k \log_e \frac{P_1}{P_r} < k \log_e \frac{P_2}{P_r} \text{ (a priori probabilities of states)}$$

or $\log_e P_1 < \log_e P_2$. That is $P_1 < P_2$ if the two definitions agree.

In a general way we can see that the more probable is the change $1 \rightarrow r$ the nearer must the configuration (1) be to (r) and thus "further" from the chaotic or most probable state. On the other hand we must not ignore that there will be usually less complexions of (1) to change from than of (2) and thus the a priori and transition probabilities will operate in opposite directions. This deduction agrees with Lewis' equation for elementary states: $P_a \varphi_{ab} = P_b \varphi_{ba}$. It should be noted that these methods are most relevant to systems which are still a long way from equilibrium and in which a degradation of free energy is going on.

It must be admitted that the above is only tentative. The choice between the two methods, if they have any value, must await the further development of physical chemistry and statistical mechanics. Until then we cannot apply them in other than the most general way to biological problems. At present I incline to the belief that the transition probabilities offer the more fruitful approach, but the entropy method has the advantage of tying up with a branch of theoretical

physics which is already thoroughly developed. The considerations of Note 1, p. 151, suggest the possibility of harmonizing the two methods.

In another place (37) these methods have been compared on a sample type of linear organization (four playing cards which continuously change from one permutation to another by simple exchanges). I find that the transition method is definitely better as it reveals the specific nature of the organization. If we look for examples in biology, they are so complex that any reasonable numerical estimate would be impossible without a great deal of investigation. In all cases the "entropy" gives a static measure of the organization. The second method gives a "historical" estimate as dependent on the factors governing changes, both past and future, in the system.

ILLUSTRATIONS OF THE TWO MEASURES OF ORGANIZATION

The nature of the difference may be understood by reference to the following cases:

(a) At a certain point of time, two zygotes, of species amphioxus (α) and species of star-fish (β) are apparently identical in chromosome structure and have undergone cleavage the same number of times; yet if we are interested in the mature starfish as end-state the blastula (β) is "highly organized" towards that end and blastula (α) not at all. An observer, ignorant of the chemical differences, would conclude that the two systems had equal "entropy" yet the future event shows that the organization is fundamentally different. In another case, the chemical constitution of the chromosome substance might be identical and the genetic difference dependent on differences in macroscopic structure. If an example of the latter could be found it would be

a more convincing illustration of the value of these methods.

(b) Consider the following physico-chemical systems:

- (1) suspensoid sol,
- (2) electrolyte solution, which can coagulate it,
- (3) emulsoid sol, protective to (1).

If the solutions are mixed in the given order, there is precipitation; if in the order 1, 3, 2, there is no coagulation. The initial entropies of the components are identical in the two cases. Entropy does not indicate the difference in final state produced by difference in time-order, just as it does not indicate why the result of mixing d-glucose and yeast should be alcohol and CO₂, though l-glucose, under the same conditions, does not change.

(c) Consider the "entropy" of a particular living animal at a certain location. This will depend among other things on probabilities P_a , P_b , P_c . . . etc. that certain food substances (a) (b) (c) . . . are present there and on the density of population of the species in that region. We should, however, come to a wrong conclusion as to the survival of the living system if we ignore the ability of the animal to search elsewhere for a missing food-stuff or to get along with a substitute.

(d) The organic property of interfering in subordinate mechanisms, when the integrity of the whole is endangered, or the interference in local processes by nervous impulses or hormone activity (initiated by central activity), which alter the conditions of selectivity, offer other examples for testing these methods.

(e) On another level we have the interference of psychological or cultural facts or stimuli in determining material distribution of the higher vertebrates (as we shall show later) and of their cultural apparatus.

THE EXTENSION OF THE ENTROPY CONCEPT

It is evident that a revisal of our prevailing method of analysis of systems will be necessary if the new measure of organization is to be introduced. This method will, however, have the great advantage of bringing to light the *significant* aspect of a structure, not simply its usefulness in producing mechanical energy. Even in the simplest of physical machines (40) the efficiency or mechanical advantage reveals only one aspect of their usefulness. The simple lever can multiply an applied force but often its real function is to change the point of application or direction of a force or moment. A lever which merely changes the point of application of a force does nothing from the point of view of energy or of entropy, i.e. from the standpoint of the first and second laws. Yet it may effect a change in biological organization. If we are considering the muscular system of an animal the entropy is eminently satisfactory but for the digestive, circulatory or reproductive systems, the dynamics is only instrumental and gives a misleading indication of their organization.

All that is necessary for our present argument is that we agree

(1) that if we take into account the biological and psychological organization of a system the probability will assume a new value and that a new kind of "entropy" will be possible; whose actual value is less important in the first place than the modification which it will introduce into our thinking. Thus it might be maintained that the "entropy" of the system on which the Maxwell Demon operates changes on the addition of the Demon to the system. His presence increases the probability that the system will become differentiated, even

before a single molecule has crossed the partition. This modification of classical entropy does not in itself involve acceptance of the "disorganization coefficient" above. Here the reference state remains as in physics but the influence of supra-molecular organization in modifying the frequency distribution of states is taken into account. To quote Lotka (22, p. 121): "a dynamics of systems comprising living matter must necessarily take account. . . . of this faculty" (the power of cheating chance).

(2) In the second place if we can use a different reference end-state another change in the "entropy" may result. The entropy concept thus extended includes entropy of "organization-for-energy-availability" as a special case.

That the value of the entropy does change in consonance with, or is a function of, the assumptions on which the probability is calculated is evident, as we have indicated above, from the new quantum statistics of the ideal gas formulated by Bose-Einstein or Fermi-Dirac (1). In the former the criterion as to what constitute separable complexions is changed—the distribution being defined in terms of *numbers* of particles in the compartments of the phase-space rather than of the more specific permutations. In the latter the Pauli exclusion principle limits the number of allowable cases and thus further departs from the classical probability. It is true that physicists can say definitely the kinds of systems where the Bose-Einstein (for radiation) or the Fermi-Dirac (for electrons and protons) statistics apply and those for which the classical statistics are adequate (at higher temperatures). However in borderline cases the validity of one system or the other is found to depend on *conventions* as to what constitutes an allowable measure of disagreement between theory and experiment.

Similarly a statistical calculation which allowed, for instance, the action of intelligent interference would necessarily arrive at different values for the entropy. This has already been examined by Szilard (32). The "measurements" of which Szilard speaks and which he regards as a prerequisite for possible entropy-decrease are similar to the "observations" of the Demon referred to earlier. I differ from Szilard in believing that the observation need not be quantitative or even crudely metrical in order to facilitate changes in the degree of organization. Szilard concludes that, as in other cases, there is compensation in the making of the observations.

The indefiniteness of entropy thus admitted into statistical mechanics is reflected in thermo-dynamics. The integrating factor $\frac{1}{RT}$ used for the equation, for a perfect gas,

$$dQ = C_v dT + \frac{RT}{V} dV$$

leads to the $\int \frac{dQ}{RT}$ which we name "entropy." However the number of possible integrating factors is infinite and hence there should be an infinite number of (physical) expressions allied to entropy. Entropy is the simplest of these (2).

Further the integral $\frac{dQ}{RT}$ includes an integration constant which can be varied according to the reference state (from which entropy differences are measured) and for this reason also the entropy can therefore assume several values. This gives some justification for my retention of the term "entropy."

The expressions obtained by using other integration constants than $\frac{1}{RT}$ do not, it is true, differ essentially—as regards their influence on the way that laws are formu-

lated—from entropy as ordinarily understood. The operations by which it is obtained are essentially the same and show the same indifference to factors which would claim the attention of a biologist or of a psychologist—factors which emerge from a system at higher levels of organization in virtue of that organization—factors which could not be predicted or identified from an examination of the elements viewed in isolation or without knowledge of the relationships into which they enter in the configuration. A good analogy in physics here would be the use of “regeneration” in a radio circuit. The current in the grid circuit depends on the geometrical form of the rest of the set-up.

KEY ACTION

An objection might be raised to our analogy between the selecting functions of the Demon and of a living organism—that the Demon acts *intelligently* so as to interfere with unfettered statistical effects. However, the duties of the Demon are both limited and mechanical as were those of Humphrey Potter attending to Newcomen's engine. It may be (we cannot escape the suggestion) that there are processes controlled by selecting agents, purely mechanical or physico-chemical in nature, which are not open to the objection that intelligence is required. Such agents would appear to produce an “un-shuffling” with reference to a predicated “purpose.” The valves of a steam engine or an internal combustion engine might, I think, be examined from this point of view. The valves perform a function similar, but not identical, to Maxwell's Demon in controlling the conversion of the uncoordinated energy of the expansion or explosion into coordinated motion. They select just the right instant for allowing the steam to impinge on the

piston head; just as the Demon selects the right instant for withdrawing the partition. The intervention is timed but the selection is made to depend on the value of a *macroscopic* parameter. The relation of an engineer with his hand on a switch to the machine controlled by the switch, or of a nerve cell to the muscle it excites, will be seen on reflection to present similar features. We have, in the past, ignored this function of automatic or semi-automatic regulators which I shall call “key” or “trigger” action. A key action is one which initiates or directs the liberation of the free energy in ways that increase the “organization” of a system or redirects already existing processes to render more probable an organization in harmony with a formulated “purpose.” In the conventional discussion of Carnot's cycle no attention is paid to the means by which the perfectly conducting and perfectly insulating walls are to be interchanged at just the right instant. This omission in the physical method renders it unable to deal with such mechanisms in organisms where coordinated intervention is universal, and illustrates the habit of physics of making certain ideal abstractions from the complex of events.

It might be pointed out that the valve, being a product of intelligence, is open to the same objection as the Demon and that the nerve is part of a living organism of whose rôle in this action we cannot be sure. We must, therefore, look for selecting processes in inorganic systems. Where in non-living matter do we find “organization” increasing, and is there in these anything similar to *key* activities?

An examination of inorganic selecting processes shows three distinct types:

(1) In filtration, diffusion through a semipermeable membrane, magnetic separation, fractional distillation, (in short the numerous methods of separation used

by the chemist), we have a separation which results in an apparent decrease of entropy. In all these cases, however, this decrease is compensated by a greater entropy increase in some other part of the system—by the decrease in the gravitational, concentration, or magnetic potential or the degradation of free heat energy. The separating agency in each case is resident in the intrinsic physical properties of the system: porosity of the filter or membrane, differential volatility of the vapors, differences in magnetic permeability, etc. (separating processes).

(2) Physical chemistry gives us many examples of periodic structures which appear spontaneously and which simulate biological organization. In the formation of certain crystals, droplets and surface films, in the chemical "garden," (produced by throwing a crystal of one soluble salt into a solution of another with which it forms a colloidal precipitate) in colloidal gels, Liesegang's rings, the fern-like crystals of lead produced in the rapid electrolysis of a concentrated solution of a lead salt or by slow reduction, the beautiful patterns in many wave-motions and in hydro-dynamic systems generally, as shown for instance in photographs of bullet-tracks. These are spoken of as static patterns but even more striking are four-dimensional configurations in flux as, for instance, wave-motion, vortex rings, or the pleasing arrangements of partials from a pipe or violin which constitute a musical note. Of the same nature, too, is the mechanism by which complex organic molecules build themselves up under favorable conditions from simple substances—as when formaldehyde gives rise to a hexose, or later to glycogen, starch and fats. All of these again are produced with entropy increase, in the ordinary way. They are the obvious examples of a much more general phenom-

enon by which the unimpeded action of electric, magnetic, molecular and gravitational fields together with the discrete structure of matter produce significant organization. The cases in which we are interested are, of course, those in which the organization is of value not in a spectacular way but as instrumental in facilitating an objective (biological) result. There is no reason why the structural units and component "mechanisms" of an organism should not arise and be maintained in response to other configurations of the same forces—(structuring agencies). The gap between these cases and those in which the same forces impel the organism in search of its food or develop its cells into useful patterns is, I believe, one of degree of complexity.

(3) Those selecting agents of which the valve is typical, influence the nature and speed of a spontaneous process. Here, again, the driving agent is the free energy of some part of the system and the entropy increases. This class covers the whole field of chemical catalysis, homogeneous and heterogeneous, hysteresis, enzyme action (microscopic) and (macroscopic) valve, choosing or gauging mechanisms of human invention. These control the rate of increase of entropy or determine in what direction the system will expend its free energy—among other things, whether the free energy will express itself first as mechanical energy or merely dissipate itself as heat. A significant feature of these is that small quantities of energy control the fate of much larger amounts. Evidently such agents, which alone of the three classes merit the name of "key" or "trigger" mechanisms, influence the probability of transition. A very instructive illustration of this principle is to be found in chemical reactions. The rate of a gaseous bi-molecular change is controlled by the fact that only molecules

whose energy is above a definite amount are "selected" for reacting. Such key-organization may either be active or only latent as in spores and other dormant biological systems.

THE NATURE OF THE ORGANIZING AGENCY

These phenomena are of importance in the light of the considerations of this paper in that they indicate some of the means by which organization of biological importance can be produced in development, growth or anabolism and emphasize the necessity of incorporating a measure of their organization into our physics and chemistry if these are ever to be able to tell us more as to the essential nature of organism than the entropy concept does at present. In organisms themselves, Lashley has given a clear insight into the nature of organization for one class of structures. "Cerebral organization can be described only in terms of relative masses and spacial arrangements of gross parts, of equilibrium among the parts, of direction and steepness of gradients and of the sensitization of final common paths to patterns of excitation. And the organization must be conceived as a sort of *relational framework* into which all sorts of specific reactions may fit spontaneously. . . ." (19). In the light of this, too, it is quite unnecessary to postulate either a "vital force," "master reaction," some very rare fluctuation or the passage of great periods of time to make possible the so-called "infinitely improbable" structures of living matter. The organizing agency is not centralized as philosophers, such as Rignano and Driesch, imagined, but is diffused throughout the whole organism in the form of residual valence, electrostatic and electromagnetic field patterns (static and dynamic), chemical affinities, potential differences, surface tension, adsorption, and in the *speeds*

with which atoms, molecules, ions, colloid particles, cells, tissues and complete organisms respond to their influences.

The nature of the mechanisms which maintain an approximately constant internal environment for the cells of a metazoon for instance, is now traceable in considerable detail to known physico-chemical processes (Cannon, 4). All three types of organizing process are probably involved in these functions. Physiologists like J. S. Haldane admit the value of these considerations but are unable to find in them a clue to the regulative action of the organism as a whole on the operation of individual mechanisms or equilibria. Only two years ago, F. G. Donnan expressed the view of the physico-chemical mechanists—who are not to be accused of any hankering after vitalistic mysticism—when he said: "The harmonious and dynamic correlation of the various organs and tissues of a living organism ever confronts us as one of the great mysteries of life." (8). A. V. Hill talks of the living cell as "a complex organized system of enzymes, interfaces, potential and osmotic differences, chemical substances *infinitely improbable in the thermodynamic sense* and yet existing in the steady state so long as free energy is available to maintain the organization." (15). The use of the word "improbable" in this connection makes the assumption that all events are equally probable and independent of each other, but this is evidently not the case.

O. Meyerhof expresses the same difficulty in these words: "One cannot understand how life can maintain itself for such long periods of time when it must, from a physical standpoint, always remain infinitely improbable." (25). Henderson (13) pessimistically concludes likewise that "the riddle surpasses us and . . . the contrast of mechanism with

teleology is the very foundation of the order of nature." I am inclined to believe that a combination of certain contemporary viewpoints makes us more able to comprehend these improbabilities and the possibility of a "chemical structure so designed as to perpetuate a perishing existence." (Leathes, 20). I shall outline below the elements on which this synthesis might rest.

Another aspect of the same problem is expressed by Meyerhof thus (25): "There is no thermodynamics peculiar to morphological processes. . . . For the formation of cell-structure, no special work is required. There is therefore no '*Strukturenergie*' into which chemical energy is converted during growth. Further, differentiation possesses no energy-equivalent nor is it correlated with an entropy decrease of the system." This statement illustrates well, I think, the tendency to over-estimate the value of energetic considerations in the analysis of a configuration. The free energy of the glycogen oxidation, glycogen→lactic acid breakdown which A. V. Hill regards as the *sine qua non* of the maintenance of structure and similar changes are the only aspects of it about which pure thermodynamics can inform us. Physical entropy does not provide a very delicate measure for structure if that structure is not adapted to or designed for making immediately available the energy of the materials of which the structure consists. For only an infinitesimal fraction of the free energy used in development or anabolism expresses itself morphologically.

THE PHYSICO-CHEMICAL BASES OF ORGANIZATION

I suggest that the fundamental difficulty is none of the above, but this: that we cannot understand yet by any symbolism

in common use the details of the method by which a dynamic structure can, so to speak, react back on itself so as to maintain itself intact or induce in neighboring lifeless matter an organization similar to its own or divide itself in such a way that the parts have latent in them the same functional possibilities as it has.

NOTE ADDED MAY, 1931: This, however, has already been done by Dr. N. V. Raschevsky in a rigorous mathematical analysis for the special case of a liquid droplet which grows by chemical interaction of substances dissolved in a surrounding medium. The work has been published in a series of articles in the *Zeitschrift für Physik* and is to appear in summary form in an early edition of the new periodical "Physics." See also the "Science News Letter" for May 9, 1931.

We have, however, some clues in, for instance, chemical auto-catalysis, in which a reaction feeds on itself because the products stimulate increased reaction of the reactants, or in Leonardo's candle flame, which shows all three of these phenomena. Life is a process or method, an integrally connected series of operations, an infectious principle of using stored free energy. The flame at any instant passes on to the flame at the next instant the secret of combustion (no secret now, when we understand to some extent such simple processes).

The picture becomes much clearer and the strain on our imagination less if we try to keep in mind simultaneously the following considerations: To begin with, the three aspects of physico-chemical structuration outlined above.

(1) Certain arrangements produce chemical separation or differentiation. Such processes may occur on a geological scale without the assistance of human supervision. Thus, the colloids of the Mississippi are precipitated when the river meets the high ionic concentration of the sea.

(2) Physico-chemical space-time pat-

terns may appear spontaneously (physico-chemical structures).

(3) The intervention of catalysts or valves (key agents) may control the rate of changes, or, more generally:

(4) We underestimate perhaps the constructive possibilities of a consistently operating selecting mechanism that "introduces order into the movements and spatial relationships of foreign molecules (and bodies) in its vicinity;" (e.g., in membrane equilibria and the CO_2 gas-liquid equilibrium in the blood). In this class, too, we must include emergent selecting mechanisms on higher levels such as the kidney. A very significant group of such mechanisms are those whose free energy changes by only small amounts but which may affect the mode of decrease of free energy in large amounts of other materials (the ductless glands). One might here suggest the rather extravagant concept of "available form" to emphasize the morphological aspect ignored when we talk of available energy alone.

(5) The specific nature of the chemical substances constituting some mechanisms will also cause a chemical selectivity. Thus it is possible that there is some correlation between the specific proteins in the chromosomes of a germ cell and the large-scale structure which arises from it through development (34).

An analogous fact which suggests some such mechanism is seen in the "biochemical adaptation" by which the proteins of antisera produced in horse blood are found on injection into dogs to become rapidly indistinguishable—by precipitation tests—from normal canine proteins (24). By other tests, this protein can be shown after three months to have retained some of the specificity of its origin. The "biochemical hybridization" of bacteria by growing them for several generations in dilute solutions of known protein—shown

by their agglutinability by precipitins specific to this known environmental protein—is another arrow pointing in the same direction (24). Apparently immunology has progressed further than other branches of biology in uncovering the specific chemical substrata of larger scale phenomena. It seems possible that this functional or structural specificity of a molecule to a particular species, is not confined to immunology but may also be found in embryology and genetics.

The "plans of the invisible architect," to use a phrase of Donnan's (8, p. 1561), are written in chemical molecular-structure—a language with a great wealth of descriptive power, as the latest edition of Beilstein shows. What I have in mind is that the functional possibilities of a germ cell will be implicit in it not as if it were a "model," on a smaller scale, of the mature organism, but in the same way as the nature of chess games is delimited by the rules which we make to govern the motion of the pieces; or, from another standpoint, as the distribution of population and industrial organization of a country is to some extent implicit in the location and extent of its natural resources, its climate distribution, its means of communication, topographical relationship to other countries and centers of industry and, in another sense, in the racial characteristics of its people, the current world picture, and the state of science, invention and religion. To use Donnan's own figure, the morphological aspect of a completed building is potentially present in the schedule of objective engineering requirements, location, costs, preferences of his client and of himself, which direct the work of the architect when he begins on his plan. These form the analogue of the germ cell organization. The embryo at a later stage might be said to be analogous to the completed plan itself.

(6) On a still higher level of organization, we have those tissues in the embryo which, when transplanted, do not adapt themselves to their new surroundings but retain their own character and force the neighboring tissue to follow them. The work of the "organizers in development" (30) has a functional similarity to selecting mechanisms and to the candle flame.

(7) The variety and large number of such qualitatively different cooperating devices found in many organisms might lead us to expect the emergence of processes of greater range and integration than in simpler configurations as, for instance, in the transition from atom to molecule.

(8) Finally, the *Gestalt* principle shows the universal tendency, even in physical systems, as Köhler continuously insists, towards organized wholes which cannot be subdivided without altering the organization throughout its whole structure and which show *unique* properties. "When two atoms come into their sphere of mutual influence. . . they either separate again or they form an orderly molecule—an *architectonic structure*—without the aid of any arrangements *ad hoc*." (17). The static charge on a conductor distributes itself in such a way that the intensity at each point is functionally dependent on the charge at all the points on the surface. The current flowing through any one conductor of a network is similarly dependent on the distribution of current in all other conductors of the network. A complex molecule like camphor, nicotine, or chlorophyll has also this quality of inviolable unity.

We pour oil into a liquid with which it does not mix. In spite of the violent interaction of the molecules at their common surface, this surface remains sharply determined, not by any arrangements enforcing this orderly distribution, but just by the play of surface dynamics between the oil and the other liquid.

If the specific density is the same for both liquids, these surface forces will change the distribution until the oil forms a regular sphere swimming in the other liquid. . . . *Dynamical interaction, undisturbed by accidental impacts from without, leads to orderly distribution, though there are no special regulative arrangements.* (Köhler, 17).

In illustrations such as these, we can see the coherence and unity of wholes which depend on the simplest of forces. How much more effective and comprehensive organization may we expect if the more complex agencies described above combine in one configuration, aided perhaps by the directive tendencies of the previous successes of the configurations to which they are genetically related and by the high individuality with which its protein, carbohydrate, and lipid molecules have been stamped by the history of the individual and of the species? The term "biochemical echoes" coined by Manwaring to describe this "imprinting" process in the formation of antibody colloids might well be extended to all cases where the experiences of the individual have been retained in his tissues. "Biological memory" (to use Rignano's expression) is both configurational and physico-chemical—the former blanket term covering our incapacity (as yet) to analyze, systematically, structure above the level of the larger organic molecules.

If and where there is an *inheritance* of such echoes, here is a likely place to look for evidence—in the modification of nuclear substances (possibly proteins, nucleic acids, lipoids, or polysaccharides) by the blood which nourishes the maturing germ cell. I doubt if the theoretical objections of Weismann and his successors could be found to be valid for some such mechanism. At any rate, it is certain he did not have this kind of "architectural shorthand" or intramolecular preformation, in mind when he wrote. Genetics assumes a dif-

ferent aspect when we take into account these intrinsic (biochemical) properties together with Woodger's "relational" (i.e., essentially configurational) properties, especially as the latter will change continuously during the whole course of development and (possibly) react with and modify the former as they change. We must be prepared to reexamine some of the central heresies of biological and medical thought in the light of this idea (34).

These same considerations may remove some of the obscurity about the origin of life which Meyerhof talks of as a "point of accumulation of improbable states." (25). The series of fluctuations necessary to produce life now appear less improbable, for the favorable fluctuations may be assisted and captured at each step by one or more of the selecting agents. And the "fluctuations" need not be microscopic only. Donnan's difficulty in connection with this theory—"What is there to stabilize and fix this rare event when it occurs?" (8)—is non-existent, for the essence of the rare configuration in which we are interested is its property of self-perpetuation.

The suggestion that I wish to make then is that all material organization, whether living or lifeless, has its roots in the same facts and that the symmetry and beauty of the products of the synthetic chemist, of geological formations, of trees, of flowers and of young girls are in essence traceable to the same kinds of designing agents.

Since first outlining the above ideas, I have found the same thought expressed by Tyndall in 1867 (35). He has just been discussing the formation, by electrolysis, of lead and silver solutions, of beautiful and striking fern-like structures. His comments must have occurred, though in less succinct form, to anyone who has performed the experiment (see, for instance, the illustrations in reference 33).

These experiments show that the common matter of our earth, . . . when its atoms and molecules are permitted to bring their forces into free play, arranges itself, under the operation of these forces, into forms which rival in beauty those of the vegetable world. And what is the vegetable world itself, but the result of the complex play of these molecular forces? Here as elsewhere throughout nature, if matter moves it is force that moves it, and if a certain structure, vegetable or mineral, is produced, it is through the operation of the forces exerted between the atoms and molecules.

Latent in these formless solutions, latent in every drop of water lies this marvelous structural power, which only requires the withdrawal of opposing forces to bring it into action.

The solid matter of which our lead and silver trees were formed was, in the first instance, disguised in a transparent liquid; the solid matter of which our woods and forests are composed is also, for the most part, disguised in a transparent gas, which is mixed in small quantities in the air of our atmosphere.

. . . And just as the molecular attractions of the silver and the lead found expression in those beautiful branching forms seen in our experiments, so do the molecular attractions of the liberated carbon and hydrogen find expression in the architecture of grasses, plants, and trees.

THOUGHT AND ORGANIZATION

I have purposely avoided the objection that the *intelligence* of the Demon is significant in his activities, but in the light of the above considerations it will surely be agreed that if we endow him with a less mechanical reaction pattern (or "habits") his organizing potentialities will be still further enhanced. This leads us to the conception that intelligent thoughts and ideas are themselves, or are parts of, selecting, key or trigger mechanisms, whether they act on single molecules or on aggregates of molecules. Effective thought represents increase of organization of idea-symbols with reference to a given problem, and if we consider the thinker and his ideas *in conjunction with the system on which he proposes to operate*, then, on a mechanistic-behavioristic basis one might say that a successful idea, indeed any act of creative thought, intro-

duces not only potentially but actually an increase of organization—probably, indeed, of the total molecular system of the thinker-ideas-materials. The change appears to be largely confined to the central nervous system and muscles of the thinker. We generally do not think of the change in connection with the rest of the system, but that is because of the atomistic viewpoint that we are trying to unlearn. Can thought then produce "entropy" decrease not only in the brain substances as Eddington supposes (he allows, 9, p. 313, the mind the ability to "tamper with the odds on atomic behavior in the brain") but also in the so-called material environment?

Organization of physico-chemical "Gestalten" consists in one sense of a linking up of fields of force between the atoms. Organization produced by mental activity will also be found to be expressible in terms of connections or bonds. Dewey (7) regards thinking as finding the missing link to place between separated or discordant elements, in particular the link that will lead most probably to the desired result, or somehow diminish the separation or discordance. All we are doing in our analysis is to give to these intangible linkages, or better—relations within the configuration, an importance comparable to that attached to, say, lines of force or potential energy in the naive physical view of the world. Many physical concepts, for instance, lines of magnetic induction or orbits in the Bohr atom, are abstractions of no more and no less reality. The justification for the statistical measures of organization which arise out of the present paper and which are applicable in principle to psychology and the social sciences lies in the fact that this arrangement of thought linkages, whether regarded as "mental" or molecular, can produce predictable and observable results no less tangible than induced

currents or spectral lines. The change in the emphasis suggested here is in harmony with the spirit of Gestalt psychology.

This discussion approaches the concept of the Gestalt from the opposite direction to that familiar to the psychologist. The configurationists do not yield to the physicist that the phenomena of pure physics have any superior claim to reality. To quote from Helson: ". . . the fact must be mentioned that thought structures are real in every sense of the word. Thinking logically is not the result of blind chance, of frequent associative connections or a matter of caprice. For the results of thinking depend not only upon thought, says Wertheimer, but *also upon the objects thought about.*" (12, p. 56). Our analysis amplifies this opinion from a new angle.

The occurrence of the thought of electromagnetic induction in the mind of Faraday affects an important transformation of one space-time pattern (1) into another (r).

(1) Certain isolated and undifferentiated ore deposits of copper, iron, graphite, etc., plus an unenlightened investigator.

(r) their later arrangement in the form of generators and electro-motors and use for the production of electric power, plus a gratified or defunct Faraday.

The thought or insight is something he can reproduce, which is probably imprinted and perpetuates itself by physico-chemical changes on certain cells (presumably) in his muscles, brain and central nervous system and later perhaps in the molecules of the written or printed word. It therefore increases the material organization of (1) with respect to (r) considered as a "purpose." Taking the physico-chemical system (Faraday + these parts of his environment containing the copper, iron, etc.) as one unit and isolated

for convenience, in the manner familiar in thermodynamic reasoning, from contiguous bodies, it is evident that the organization of this unit becomes greater in a minute but very vital respect the instant the intuition appears in the mind of Faraday. In short, can we not say that the "generalized entropy" (as we have described it) decreases during thought in which decisions are made? There is nothing in this analysis to show that the classical entropy decreases. From another point of view, the arrangement simply becomes more "known." However, the second law takes on an indefiniteness it did not previously have.

The instruments of the organization process may thus be resident in the special distribution or physical interconnections of matter, as for instance in telephones or protoplasm; but also and most significantly in the idea or theoretical scheme which can unite in a new way distinct, in-harmonious or heterogeneous material—whether inorganic or living.

The nature of the influence of thought on organization becomes more easily apprehensible if we abandon the mechanical-atomistic standpoint and, using the Gestalt concept, frankly admit the morphological aspects of experience into theory. "The inner necessity pervading the entire structure does not come from the mere relation of part to part. . . . but rather springs from the peculiar nature of the whole which is more or less autonomous." (12). We are helped in this by our very uncertainty as to the location of the Gestalt. "There are physical, physiological, biological and psychological (and logical) structures possessing properties *not compoundable from their parts* and hence to be regarded as configurations (p. 364). . . . so it is impossible to fix precise meanings for the concept of *Gestalt* when we examine it closely in its

various uses in the configurational literature." (p. 368) (Helson, 12). By treating the psychological fact as an integral part of the physical picture, we help break down the barrier between these apparently conflicting interpretations.

There is a weakness in the above analysis with its apparently sudden change in the organization. The "insight" presupposes a discontinuity ("*Einschnappen*") which does not, in fact, occur. The insurgent factor is regarded as a foreign element which suddenly and mechanically intrudes itself upon a structure more or less unprepared for it. As matter of "fact," however, the apparently "improbable" emergence of an intuition, as indeed of all configurational integrations, is due to the growth or decay of the pattern according to definite laws which would be clearer to us if we could discover all the factors operating and adequately apprehend their interconnections. Here again as with the "accidental" first beginnings of life, the outcome is inevitable and explicable. The thought "emerges" from the Gestalt as a necessary result of the presence in it of the elements concerned in their given relations much as a new complex organic compound appears in the mixture of materials from which it is synthesized by the chemist. For the Gestalt is a *dynamic* organization in constant flux. To quote Helson again: "Configuration connections are not the results of frequent associations or blind juxtapositions, but are inner bonds imposed by the demands of the total structure." (12, p. 54). And at another place: "Configurations become more articulate or more finely structured, simpler in form, more precise or less definite, poorer in form or chaotic. What is to be singled out. . . . will depend upon. . . . a number of. . . . factors like coherence, persistence and impressiveness. In gen-

eral, the progress of configurational change is from chaotic groups of elements, at the one extreme (really a minimum of 'structuration') to more and more complex structures." (12, p. 369).

From one point of view, the "entropy" of all the coal and oxygen in the world might be regarded as changing at the time of James Watt's invention by a small but finite quantity. The "entropy" of any given mass of coal changed by an amount which depends on the probability that that mass will be brought into connection with an engine. The existence of the engine (or of the idea of the engine) apparently increases the chance of our using the coal for producing mechanical work; that is, according to our limited insight into history. Looked at after the event, the engine, though "infinitely improbable," was the inevitable outgrowth of the contemporary world and its instrumentality in unlocking free energy was certain.

It might be well to modify the above treatment in the light of Whitehead's picture of the organism (38). We have assumed a succession of instantaneous three-dimensional configurations with no overlapping, but organism cannot be separated from the concept of functioning: the successive events constituting the organism themselves form a configuration in space-time. The same idea is applicable to our heterogeneous system—organism plus material environment. We should really reread the above as dealing essentially with a four-dimensional configuration with less emphasis on the serial relation of "simultaneous" snapshots.

THE USES OF INTUITION

I do not wish it to be supposed that I exaggerate the value of this extension of

the thermodynamic method. With Woodger (39) I believe that the development of special ways of thinking about the facts in terms of suitable symbolism promises more in the end. However, that is no reason why the physicist should not try to bridge the gap and to present the biologist with his physical tools in as effective a form as possible.

There is a school of thinkers in psychology, sociology and history (Klages, Hyde, Friedel) which suggests that we may be premature in expecting the same kinds of verifiability and reproducibility there, that we are accustomed to in physics. An intelligent use of intuition by the most informed and profound minds appears to have more significant contributions to make to complex problems than the methods of symbolic analysis or controlled experiment alone. Thus Goethe and Nietzsche were good psychologists. In the deeper regions of truth, universal consent is not a very helpful guide. Indeed have the fundamental theoretical developments of science ever rested on widespread understanding? In virtue of the similarity of some of its problems to those of psychology, it may be that this concession is required in biology. There is nothing essentially unscientific about such a procedure, for the judgments of such men can be formed in the light of carefully analyzed experience. Also our agreement as to the truth of mathematical propositions, on which so many physical proofs are based, is largely intuitive in origin. I am arguing for the admission of intuition at another point in the chain of logical connections, where it may have equally important results.

LIST OF LITERATURE

- (1) BIRTWHISTLE, G. The New Quantum Mechanics. 1928, chap. 28, 29.
- (2) BRENNEN, W. J. At meeting of Amer. Chemical Soc., Spring 1929.
- (3) BRIDGMAN, P. W. The Logic of Modern Physics. 1928, p. 3.
- (4) CANNON, W. B. Organization for physiological homeostasis. *Physiol. Rev.*, 1929, ix, p. 399.
- (5) CONDON, E. U. Book review of Frenkel: Einführung in die Wellenmechanik. *Physical Rev.*, 1929, 34, 1065.
- (6) DARROW, K. K. Recent statistical theories. *Bell Tel. Jour.*, 1929, VIII, p. 675.
- (7) DEWEY, J. *How We Think*. 1909, chap. 6, p. 72-3.
- (8) DONNAN, F. G. The mystery of life. *Jour. Chem. Educ.*, 1928, 5, p. 1564, 1569.
- (9) EDDINGTON, A. S. Nature of the Physical World. 1929, p. 314.
- (10) FRY, C. J. Probability and Its Engineering Uses. 1928, p. 118.
- (11) GRAY, J. The kinetics of growth. *Brit. Jour. Exp. Biol.*, 1928, VI, p. 267.
- (12) HELSON, H. The psychology of gestalt. (Reprinted from *Am. Jour. Psych.*, 1925-26). 1925, 36, p. 364-9; 1926, 37, p. 56.
- (13) HENDERSON, L. J. The Order of Nature. 1925, p. 209.
- (14) HERZFELD, K. F. Muller-Pouillet's: Lehrbuch der Physik, III, Kinetische Theorie der Wärme. 1925, p. 113-126.
- (15) HILL, A. V. The maintenance of life and irritability in tissues. *Nature*, 1929, 123, p. 727. (Supplement.)
- (16) KOENIGSBERGER, L. Hermann von Helmholtz. 1906, p. 40-41.
- (17) KÖHLER, W. Gestalt Psychology. 1929, p. 138.
- (18) KRIKORIAN, T. H. The meaning of purpose. *Jour. Philos.*, 1930, XXVII, no. 4, p. 99.
- (19) LASHLEY, K. S. Basic neural mechanisms in behavior. *Psych. Rev.*, 1930, 37, p. 23.
- (20) LEATHES, J. B. Function and design. *Nature*, 1926, 118, 519-522.
- (21) LEWIS, G. N. The symmetry of time. *Science*, 1930, LXXI, p. 572.
- (22) LOTKA, A. J. Elements of Physical Biology. p. 34, 35, 121.
- (23) MACH, E. The Forms of Liquids, in Popular Science Lectures. 1894, 1910 Ed., p. 14-15.
- (24) MANWARING, W. H. Biochemical relativity. *Science*, 1930, LXXII, p. 25.
- (25) MEYERHOF, O. Thermodynamik des Lebensprozesses. *Handbuch der Physik*, XI, 1926, p. 240.
- (26) RASCHEVSKY, N. V. Zeitlichen Verlauf der Thermodynamischen Prozesse. *Zeit. für Physik*, 1929, 54, p. 736.
- (27) REISER, O. L. Probability, natural law and emergence. *Jour. Philos.*, 1926, XXIII (16) p. 423.
- (28) SCHOTTKY, W. Statistischen Fundamentierung der Chemischen Thermodynamik. *Annalen der Physik*, 1922, 68, p. 516.
- (29) SMOLUCHOWSKY. *Phys. Zeitschr.*, 1912, 13, p. 1069.
- (30) SPEMANN, H. Organizers in animal development. *Proc. Roy. Soc. Lond.*, 1927, 102B, p. 180.
- (31) SULLIVAN, J. W. N. The Bases of Modern Science. 1928, p. 21.
- (32) SZILARD, L. . . Entropieverminderung. . . bei Eingriffen intelligenter Wesen. *Zeit. für Physik*, 1929, 53, p. 840.
- (33) TAFT, R., AND STARECK, J. Growth of lead crystals in silica gels. *Jour. Chem. Educ.*, 1930, 7, p. 1520.
- (34) TAIT, J. Homology, analogy and plasis. *QUART. REV. BIO.*, 1928, 3, p. 151.
- (35) TYNDALL, J. "Matter and Force," in Fragments of Science. 1867, p. 392-3. (Burt).
- (36) WATSON, D. L. Entropy and organization. *Science*, 1930, LXXII, p. 220-222.
- (37) ———. The physico-chemical measure of organization. In preparation, outlined Amer. Chemical Soc. meeting, Sept. 1930.
- (38) WHITEHEAD, A. N. The Principles of Natural Knowledge. 1925, p. 3.
- (39) WOODGER, J. H. The concept of organism. *QUART. REV. BIO.*, 1930, V, p. 4.
- (40) ———. Some problems of biological methodology. *Proc. Aristotelian Soc.*, 1929, p. 336.



DEATH AND ITS CAUSES

By W. W. LEPESCHKIN

From the laboratories of the Desert Sanatorium and Institute of Research

PART I. DEFINITION OF THE CONCEPTION OF DEATH

THE problem of death and of the processes which bring it about has attracted the attention of naturalists during the last twenty years. This attention was due, on the one hand, to the appearance of some new papers devoted to the reproduction of Protozoa, and, on the other hand, to the publishing of several experiments on the artificial culture of tissues and organs. In the monographs dealing with the problem of death, it was united with the problem of senescence. Their authors therefore considered exclusively the problem of so-called natural death, because it was of special interest to the widest circles of readers. In order to understand death it is, however, necessary to consider a more general problem dealing with the process of death independently of whether it is only a consequence of growing old, or whether it is produced by some direct harmful effect of the surrounding medium.

Death never occurs instantaneously. The problem of death involves, therefore, the problem of its gradual development or necrobiosis, which may result as well from normal life as from latent life or anabiosis, if it lasts for a long time. In this part of my paper I shall try to define the conception of death in its general meaning.

The common-sense conception of death

In the common speech death is considered as an irreversible loss by the organ-

ism of the property of being alive, that is of showing growth, development, metabolism, movement, and reproduction, which, in the total, form life.

Using this simple definition of death we experience difficulties however, if we consider the death of multicellular organisms. Indeed, life is not anything restricted to one part of the organism; it represents a summarized action of innumerable single processes proceeding in different cells of the organism. As single cells die at different times, one is not certain what moment of the necrobiosis should be defined as death.

In order to avoid this difficulty, Jores (1910) proposed to define death as a complete stoppage of life activities in every part of the body. On the other hand, it is well known that single cells can die in a quite healthy organism. A considerable number of scientists who investigated the process of death (Cohnheim, 1882; Ribbert, 1908; Verworn, 1922; Minot, 1908; etc.) arrived therefore at the conclusion that death represents only a phase of the development of an organism. According to Lipschütz (1915), death is the last link in a long chain of changes which are carried out in a living organism. Schäfer (1913) affirms even that death is the last act of life, while Tangle (1916) considered it as a necessary part of every life, because, according to him, every physiological process becomes possible only when some amount of "living substance" is annihilated. We see therefore that no agreement was reached in the opinions of

scientists with respect to the definition of the death moment of multicellular organisms.

Death as the annihilation of an individual

We have also difficulties in our endeavor to find a good definition of death if we try to adjust this definition to our conception of an individual.

One understands by the word individual mostly a part of the living world which can not be divided into smaller parts without an annihilation of life. According to this opinion, every organism represents an individual, and as only individuals are able to support their life themselves, one concludes that the annihilation of an individual must be accompanied by death. This opinion, in its application to unicellular organisms, leads to the admission that the reproduction of these organisms is accompanied by death. Such an opinion was recently expressed, for instance, by Doms (1921), who considered death as an expiration of the individuality representing a "primary adequate system". A similar but somewhat modified opinion we find in Hartmann's work.

As is known, Weissmann (1892) pointed out that death is characterized by the appearance of a corpse. Disagreeing with Weissmann, Hartmann (1906) affirmed that the death of protozoa is not accompanied by the appearance of a corpse, which is observed only in the case of the death of multicellular organisms. According to Hartmann, death is in all cases a completion and stopping of the individual development. In the case of unicellular organisms, this stopping occurs simultaneously with their reproduction. At the same time, considering the death of single cells in the multicellular organism and necrobiosis, Hartmann emphasized that he understands by the development of an organism not only a constructive, onto-

genetic, but also a destructive, degenerative development constituting necrobiosis.

For every modern physiologist it is evident that the life processes do not stop at once after an annihilation of the individual. Many experiments of late years gave striking examples of survival of different animal and human organs. I should like to cite, for instance, the interesting experiments of Kravkov (1922), who succeeded in keeping severed human fingers alive for several months. It proved possible to keep also other severed organs in the living state, as for instance, ears, head and heart (Pissemsky, Kuliabko and others). Moreover, single tissues and cells of animals and plants can be cultivated in artificial solutions, as was shown by Leo Loeb (1908), Harrison (1913), Carrel (1921) and others. Especially interesting are the well known Carrel experiments on the artificial culture of the tissue from the heart of chicken embryo. This tissue is still living at a much greater age than the life span of an intact fowl.

Verworn's hierarchy of individuals

Verworn tried to reconcile the cited observations with the above opinion concerning the necessity of death (that is of stopping of life) after an annihilation of the individual. He proposed to admit that there are individuals of different kinds. Single cells represent, according to Verworn, individuals of the first order. The individuals of the second order are tissues; those of the third order are organs; those of the fourth order are organisms and those of the fifth order are states. The division and transformation of the individual of one kind into the individuals of the other kind is not accompanied by death, but the annihilation of the individual of the first order brings it about.

This compromising opinion seems to me, however, not satisfactory, because, first,

it rejects the usual conception of an individual as an independent organism. Second, it does not set aside all difficulties in the definition of death. Indeed, the moment of death of multicellular organisms does not become more distinct if we adopt Verworn's ideas, namely, we do not know how many individuals of the first and second orders should be dead in order to conclude that the individual of the fourth order, that is the organism, is also dead. Third, it is scarcely correct to assert that life is bound up with the individuality of Verworn's first order, and that the annihilation of this individuality necessarily brings about a stoppage of all physiological phenomena. Indeed, the living matter of the cell consists of protoplasm (cytoplasm), nucleus, chromatophores (plants), fibrils (animals) and other cell organs. It is now proved that protoplasm can be separated from nucleus and remain alive after such separation for a long time. Gerassimoff (1902) showed, for instance, that the cooling of *Spirogyra* at night produces cells which have no nucleus and which, in spite of this, can live for more than two weeks, and perform their physiological functions almost as well as before. The same phenomenon is known for erythrocytes of mammalia, which lose their nucleus soon after their formation and can live sometimes for several weeks. The experiments of Prowazek (1904) and others on the regeneration of protozoa proved also that a piece of the cell containing no nucleus can show sometimes not only metabolism and movement, but also regeneration. A piece of the cell, like surviving organs, can be therefore alive for a long time, and the disappearance of the individuality of the first order does not necessarily bring about death. It does not matter that the separated parts of the cell can live only for a time, because we know complete cells

which can live only for a short time (unfertilized generative cells, for instance). The observation of the death of the cell shows also that its different parts do not die simultaneously. The nucleus dies, for instance, sooner than protoplasm, etc. Thus, if we adopt the Verworn idea and consider the experiments cited above, we must call the living protoplasm separated from the nucleus an individual of an order smaller than one. At the same time, protoplasm can be cut into pieces and does not die after such treatment; we must therefore admit the existence of individuals of a still lower order than that of protoplasm. The Verworn row of individuals may become therefore very long.

We see that Verworn's ideas of individuality do not help us to define the moment of death in the case of multicellular any more than of unicellular organisms. Thus, I do not find any reason why we have to renounce the conception of an individual as an independent organism. Only this definition of individuality is comprehensible and should be considered in our discussions concerning the moment of death. But this of course, does not mean that I agree with the definition of death as an annihilation of the individual. On the contrary, I think that such definition of death contradicts our customary opinion that dead organisms do not show any life phenomena, or at least, that these phenomena are restricted to some tissues or cells which are not important for the life of the whole organism.

One can not deny that the cell division of unicellular organisms means an annihilation of one individual and its transformation in to two new individuals. At the same time, the life processes are not at all depressed by the cell division. They continue uninterrupted in both parts of the cell, and in both new individuals. We have therefore no reason to conclude that

any death occurs when a cell divides itself into two cells. On the other hand, death is not always accompanied by an annihilation of the individual, and we could speak of the death of single organs, tissues, or cells and even of the death of living matter, as occurring in a quite healthy organism, which retains its individuality completely. Therefore there is good reason to believe that individuality and death are independent of each other. In order to avoid contradictions we have to define the conception of death independently of any idea of individuality.

Death as the end point of necrobiosis

We may consider first the death of multicellular organisms. I have emphasized above that this death does not occur all at once, but develops gradually, although the development of death or necrobiosis sometimes proceeds very quickly, as for instance in the case of small organisms affected by high temperature or very poisonous substances. It is evident that we can say that death is either this slow or quick process itself or some of its phases. In the first case the word death will have the same meaning as the word necrobiosis, and then we should not be able to speak of "the moment" of death. Furthermore we should have to admit that the organism is dead at the beginning of necrobiosis, that is when most physiological processes are normal.

Hence the only way to find a correct definition of death is to consider the second case, that is to call one phase of necrobiosis death. But what phase could it be?

It is evident that we could not call death the beginning of necrobiosis. Should we call it some intermediate phase of this destructive process? In this case we should have to be prepared to admit that our organism may sometimes revive (after

an adequate treatment), that is, we should consider death as a reversible phenomenon, which would be not in accord with our definition of death as an irreversible loss of the property of being alive. Moreover, we should admit in this case that in the dead organism some life processes must be carried on.

The best way to avoid all these contradictions is, according to my opinion, to differentiate between a theoretical and a practical definition of death. The theoretical one should be adjusted to the requirement that dead organisms can not revive or show any physiological phenomena. According to this definition, one could consider only the end phase of necrobiosis as death, that is, the organism could be called dead only if all its living matter is dead.

The practical definition of death should also be in accord with the requirement that dead organisms can not revive, but it may be admitted in this case that some physiological processes can proceed in dead organisms. I should like to suggest, for instance, that physicians may regard a man whose heart has stopped as practically dead if some evidences of a bacterial destruction become distinct (corpse smell, formation of hydrogen sulphide in the mouth, etc.). By this definition of death the burial of living men who are in the state of lethargy would be avoided, and the restoration of men to life after injection of adrenaline into their heart would be easily explained.

Concerning unicellular organisms, their death occurs under the same conditions as the death of multicellular ones. If these conditions become unsuitable for life, as for instance, when some poison is added to the culture solution, or the temperature is too high, the growth becomes slower and finally stops, because the living matter filling the cell gradually dies. Even a

lack of food produces a stoppage of growth and a necrobiosis of all unicellular organisms, because they can not be kept alive forever if their growth has stopped, although some of them take the state of anabiosis under such conditions. The gradual dying of unicellular organisms after the stoppage of growth may be compared with the growing old of the multicellular organisms. In both cases a necrobiosis finally develops which leads to death. If living matter is not renewed, it dies at length.

The difference between unicellular and multicellular organisms is only in the more complex organization of the latter. We have not yet any means to prevent the growing old of higher organisms because we can not induce them to grow and to renew their living matter, and especially to renew the living matter of their nervous system. On the contrary, in the case of unicellular organisms, we can do it by removing poisons from the culture solution and by providing them with food. Under such a condition they do not cease to grow and do not stop cell division, and neither necrobiosis nor death is observed. It does not mean, however, that the unicellular organisms are eternal, because their death does not appear as long as the conditions of life are suitable. In reality, such conditions could not exist on the earth for all individuals: their reproduction is so enormous that all food on the earth is not sufficient to maintain the life of all unicellular organisms. The simplest multicellular organisms, as for instance, radiolaria and polypes, behave like unicellular organisms because, thanks to their small size and the liquid medium in which they live, the removal of poisons and the providing with food can be easily performed.

On the other hand, as was already mentioned, the living matter included in the

cell of unicellular organisms dies gradually, that is, shows a necrobiosis. Therefore there is good reason to believe that these organisms do not differ from multicellular organisms in their death, and we shall not make a mistake if we admit that the theoretical definition of the death of unicellular organisms is the same as that of multicellular organisms, that is, death is an end phase of necrobiosis, and the organism can be called dead only if all its living matter is dead. As to the practical definition of death, it is not necessary in this case.

On the basis of the definition of death adopted in this paper we may conclude that the reproduction of unicellular organisms is sometimes but not always accompanied by death, namely when not the whole cell but only its part is transformed into new cells. In this case the remainder of the cell dies, as for instance, in the case of the formation of spores of yeast, etc.

The above definition of death as a death of all living matter of an organism permits us to speak of the death of single organs, tissues and cells of multicellular organisms without any alteration of our present idea of an individual as an independent organism. Indeed, if the living matter of a cell dies completely we may say that the cell dies. If all cells of a certain tissue are dead, we shall call this tissue also dead, and if all tissues of an organ are dead, we shall consider this organ as dead. The theoretical definition of the death of multicellular organisms may therefore be modified as follows: their death is the death of all their cells, tissues and organs.

PART II. THE CAUSES OF THE DEATH OF LIVING MATTER

In the first part of this paper I pointed out that the death of organisms, tissues and cells is first of all the death of living

matter. I proposed to consider the death of every organism as an end phase of necrobiosis, that is, to call an organism dead only if all of its living matter is dead. This was my theoretical definition of death. At the same time I proposed also a practical definition which could be used, for instance, by physicians. In this part of my paper I am going to discuss the causes of the death of living matter.

When one speaks of the cause of the death of living matter one must remember that, although the opinions of medieval naturalists (Galen, Fernellius, Descartes), that some soul or *pneuma* leaves the body of an organism and causes death, were abandoned long ago, the ideas of vitalists (Bordeu, Barthez, Chaussier and others) or their modifications still are defended by several scientists. Temporarily, I leave these ideas undiscussed, and we shall see afterwards that they are not important for the solution of the problem of death. On the other hand, some theories should be mentioned which consider the cause of death from a purely mechanical or chemical standpoint. To the theories of this kind belongs Pflüger's theory of a living protein. This theory originated in the second half of the nineteenth century soon after the publication of the well known works of Miescher and Hoppe-Seyler, in which the results of the first chemical analysis of living matter were described. This analysis showed that living matter contains much "albumen substance."

Pflüger (1873) supposed that living matter contains "living protein" which differs from dead proteins of our laboratories by a peculiar structure of its molecules. These molecules contain, according to Pflüger, the cyan group, while the molecules of dead protein contain ammonia radical, that is, the amino group; the former is unstable and is very easily

transformed into the latter. This transformation, according to Pflüger, causes death.

Verworn (1903), who seemed to adopt Pflüger's theory, substituted the word "biogen" for "living protein," ascribed a great instability to it and compared it with explosive substances. Its decomposition can be produced, according to Verworn, even by stimuli.

The biogen hypothesis was adopted also by Detmer (1882), who supposed that the molecule of this substance is decomposed in the process of metabolism and transformed into a nitrogen compound and a substance which contains no nitrogen. This decomposition, together with the change of the structure of protein molecules, causes death. A like theory of the peculiar chemical structure of living matter was developed also by Allen (1899).

Coagulation and death

On the other hand, Berthold (1886) ascribed death to an irreversible change of an equilibrium and of a distribution of substances in the cell. A coagulation of proteins plays, according to Berthold, an important part in this change. That a congelation and coagulation accompany death was clear also to other scientists, as for instance, to Pfeffer and Arth. Meyer. The application of colloid chemistry to the interpretation of the structures visible in the cells permitted me to regard the changes in living matter accompanying death as a colloid-chemical phenomenon. In my papers devoted to the structure of protoplasm and to the causes of death (1910, 1911, 1912, 1924) I pointed out that living matter, which represents, in active state, a colloidal solution, coagulates simultaneously with death. This coagulation is proved by the congelation of liquid living matter and by the appearance of granules in it. Even in the cases where

living matter apparently looks homogeneous after the fixation (that is, a quick death), an investigation with the ultra-microscope or staining proves the appearance of minute granules in it. The well known structures found sometimes in dead protoplasm (fibrous, net-like, and froth-like structures) are only coagulation structures observed also in coagulated colloids. Moreover, I pointed out that living matter loses its selective permeability after death, that is, it becomes easily permeable not only to lipoid soluble substances but also to all substances soluble in water. This increased permeability of dead protoplasm is comprehensible, because the liquid protoplasm, easily dissolving lipoid soluble substances, becomes transformed into a coagulation jelly consisting of granules mostly visible under the ordinary microscope. Through the pores of this jelly all substances soluble in water penetrate as easily as through the pores of a sponge.

Chemical changes in death

On the other hand, it is well known that in some cases protoplasm partially or completely dissolves in the surrounding water if it is injured or killed, as for instance, in the case of red blood corpuscles, which often show a hemolysis under the conditions which usually bring about death. In the case of colorless cells this process is often called cytolysis. Therefore not only a coagulation but also a solution of the substances composing protoplasm is characteristic of death. This solution is usually explained by assuming that the surface of protoplasm is covered by a thin film (protoplasm skin, *plasmamembran*) which becomes injured to such an extent that it becomes permeable to substances contained in the inner parts of protoplasm. My investigations (1910, 1913, 1923, 1924, 1925, 1926) proved,

however, that there is no film on the protoplasm surface which could prevent the diffusion of substances from the cell. The pellicle covering the surface of the red blood corpuscles is easily permeable to hemoglobin, in spite of the fact that the hemoglobin comes out from the cell into the surrounding water only after the corpuscles are injured or killed (1924). At the same time my investigations showed that there is no stroma in living protoplasm on which the diffusing substances could be adsorbed and which could be freed after death. The only correct explanation of solution of protoplasm in the surrounding water after death is therefore the supposition that some chemical changes, which free the diffusing substances, occur in protoplasm simultaneously with death.

Indeed, there is some evidence that death is accompanied by a chemical decomposition of substances forming protoplasm. In one of my previous papers (1928) I cited this evidence. It is proved that protein substances and lipoids are not free in living protoplasm, but become free (sometimes only partially) after death, and that, at the same time, lipoids are maintained in living protoplasm by protein substances. I stated therefore that protein substances and some lipoids are probably combined with each other in living matter, but their compounds, which I called principal compounds, are very unstable and decompose under the influence of different harmful effects.

Detmer's opinion, that "biogen" decomposes to a nitrogen compound and a nitrogen free substance, is therefore near my opinion. At the same time, Pflüger's idea of the different chemical structures of the protein molecule in living and dead protoplasm is wrong, because, according to Emil Fischer's investigation of proteins, their molecule contains no cyan group.

The substance which would contain this group instead of the amino group could not be called protein.

Thermic effects of death

It was mentioned that the principal compounds forming living matter are very unstable and decompose even under the influence of a relatively slight mechanical effect. As the decomposition of very unstable chemical compounds is usually accompanied by the production of heat, we may expect the decomposition of the principal compounds of living matter and death to represent an exothermic process. Indeed, my experiments (1929) have shown that the death of yeast cells is accompanied by the production of heat. The thermic effect observed in this case is about 2 gm. calories per gram of dry substance, and is therefore small as compared with the heat produced in most exothermic chemical reactions (calculated per gram of the decomposing substance). On the contrary, if we try to determine the heat produced by the decomposition of one molecule of the principal compounds composing living matter we will find that this heat is very great, because the molecular weight of these compounds is evidently greater than that of protein substances. Among these substances hemoglobin is one the molecular weight of which is determined. It is at least 16,700. The heat produced by the decomposition of one molecule of the principal compounds of living matter is therefore greater than 40 kilo calories, while the heat produced by the decomposition of one molecule of nitrogen chloride, that is, of one of the most unstable explosive substances, is only 38 kilocalories, etc. In my recently published experiments on red blood corpuscles I found the same thermic effect produced by their death or hemolysis (1930). This explains the great instability of the principal

compounds of living matter, which could be compared only with that of most unstable explosive substances.

There is therefore good reason to believe that the death of living matter is accompanied by a decomposition of some very unstable chemical compounds, it being very probable that these compounds (principal compounds) are formed by protein substances and lipoids. On the other hand, there is some evidence that these compounds play an important part in the formation of the dispersion medium of protoplasm and of living matter in general (see my paper cited above). Hence, the decomposition of the principal compounds brings about a destruction of this medium. Indeed, I found that in all investigated cases this medium is replaced by water, which fills the channels of the coagulation jelly of protoplasm after its death. The destruction of the dispersion medium of protoplasm after death easily explains the congelation of liquid protoplasm. Indeed the products of the decomposition of the principal compounds forming this medium are mostly insoluble in water, and are precipitated in the form of granules. These granules join the granules of the colloidal substances which have been dissolved in living protoplasm and become precipitated after their dispersion medium was destroyed.

On the contrary, if the products of the decomposition of the principal compounds forming the dispersion medium and the substances dissolved colloiddally in protoplasm are soluble in water, or at least, if some of these substances are soluble in it, no coagulation, or only a partial coagulation of protoplasm is observed. At the same time, the whole mass or a part of protoplasm dissolves in the surrounding water. But even in these cases it is possible to bring about a marked coagulation of protoplasm if the cells are killed by

poisons which form insoluble compounds with the products of the decomposition of the principal compounds and with colloidal substances dissolved in protoplasm. This occurs, for instance, after the action of corrosive sublimate, which does not produce any hemolysis of red blood corpuscles or cytolysis of colorless cells, if taken in great concentrations.

If the dispersion medium of a colloidal system is destroyed, the whole system is evidently destroyed. As the chemical agents of the cell and the materials which are used in metabolism are dissolved or colloiddally dispersed in liquid living matter, they may dissolve after death in the surrounding water or be adsorbed by the coagulated substances. They may be also precipitated in non-dissolved state after death. In every case they become lost for the cell, because only chemical reactions between substances dissolved in living matter are important for its metabolism. Hence, we may expect the chemical reactions forming metabolism to stop or to be modified to such extent that they could not be of any use for the cell. But if metabolism stops, the other life processes must also stop, because they are closely connected with metabolism. It is well known that growth, movement and reproduction are most sensitive to all changes of metabolism. They are sometimes especially sensitive to the changes in the oxygen metabolism, and stop at once if it ceases.

Is death the result of chemical and physical processes?

We arrive therefore at the conclusion that if the principal compounds of living matter become decomposed, life must stop. We now may ask whether this decomposition and the destruction of the whole colloidal system of living matter result from chemical and physical processes in it,

or are produced by a withdrawal of some kind of soul or by an annihilation of a living force, etc.

In order to answer this question we may keep in mind that the principal chemical compounds of living matter which are present in its dispersion medium are so unstable as to be compared to explosive substances. On the other hand, it is well known that explosive substances can be decomposed by mechanical effects, by high temperature, sometimes by very strong light, and by all chemicals which act on different parts of their molecule. The destruction of the dispersion medium and of the whole colloidal system of living matter is produced by the same factors, that is, by mechanical effects, by high temperature, sometimes by very strong light, and by all chemicals which react with their component parts, that is, with protein substances and lipoids. Protein substances are chemically altered by acids, alkalies, salts of heavy metals, high temperature and strong light. All these agents produce death. All agents which alter lipoids chemically (for instance, saponin and iodine) also produce death.

It is therefore proved that all agents which produce a chemical alteration of the component parts of the principal compounds of living matter bring about their decomposition and the destruction of the whole colloidal system of protoplasm. Thus it is evident that in the case of the action of the above mentioned agents on the cell, death is brought about by the chemical alteration of the component parts of living matter, and is therefore independent of a soul or other unknown mystic phenomenon. The chemical alteration produced by the mentioned agents is quite sufficient to produce death. Hence, if somebody thinks that the soul or any vital force, etc., cause life he must admit that both leave the cell in this case because life

can be no more maintained in dead protoplasm. First living matter dies, then soul, etc., leave the cell.

If we consider now the other cases of death, we shall come to the conclusion that they are produced mostly by poisons which are accumulated in tissues or in the surrounding medium, as, for instance, the death produced by many pathogenic parasites and in general by toxins, by suffocation and by saturation of the surrounding medium with decomposition products formed in metabolism. It is certainly unknown how all these poisons bring about the decomposition of the principal compounds of living matter, but it would be quite incomprehensible if they act first on some mystic part of living matter in this case. It is more probable that in all cases poisons act on the component parts of the principal compounds chemically or produce a coagulation in protoplasm which acts mechanically on these compounds and causes them to decompose.

Natural death

Concerning so-called natural death, that is, death which occurs apparently without any change in the surrounding medium, or in the life and state of an organism, it is caused sometimes by a gradual poisoning of the cells, sometimes by a spontaneous decomposition of the principal compounds. A spontaneous slow decomposition is known for all unstable substances,

as, for instance, for explosives. In the case of unicellular organisms natural death occurs if life processes are caused to stop by a very low temperature, drought, or want of food. The state in which the organism is in this case is known under the name of anabiosis. The principal compounds of living matter, being very unstable, must slowly decompose if their supply in the cell is not renewed by metabolism. Only in the case of very low temperature at which all chemical reactions stop, the decomposition of the principal compounds could almost stop too, and living matter could remain alive for a very long time even if it were not renewed.

In the case of higher organisms natural death is known to occur as a result of a gradual death of the nervous system. The causes of this death probably lie in a poisoning of the nervous cells by the decomposition products of metabolism and also in a spontaneous decomposition of the principal compounds of living matter.

It is therefore very probable that in all cases death is caused by the decomposition of these compounds and by the succeeding destruction of the whole colloidal system of living matter. If one should like to suppose that every organism possesses a soul, living forces or other mystic part, one must admit that they leave the body after death because of the impossibility of life in it, but they do not produce death themselves, by leaving the body.

LIST OF LITERATURE

PART I

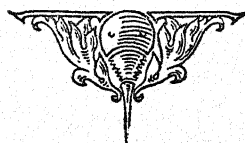
- COHNHEIM. 1882. Vorlesungen über allgemeine Pathologie. 2te Aufl. Berlin.
- DOMS. 1921. Ueber Altern, Tod und Verjüngung. Z. f. ges. Anatomie, 23, 250.
- GERASSIMOFF. 1905. Bull. d. l. Soc. Natur. d. Moscou.
- HARTMANN. 1906. Tod und Fortpflanzung. München.
- JORES. 1910. Wann ist ein Lebewesen tot? Umschau, 14.
- KRAVCOV. 1922. Zeitschr. f. exper. Medizin, 27, 127.
- LIPSCHÜTZ. 1915. Allgemeine Physiologie d. Todes.
- MINOT. 1908. The Problem of Age, Growth and Death. New York, London.
- PROWAZEK. 1904. Beiträge z. Kenntnis d. Regeneration d. Protozoa. Arch. f. Protistenkunde, 3, 57.
- RIBBERT. 1908. D. Tod aus Alterschwäche. Berlin.
- SCHÄFER. 1913. D. Leben, sein Wesen, sein Ursprung und seine Erhaltung.

WEISSMANN. 1892. *Ü. Leben und Tod*. Jena.
 VERWORN. 1922. *Allgemeine Physiologie*. VII.
 Aufl.

PART II

ALLEN. 1899. What is life? *Proc. Birmingh.*
Natur. Soc., 11, 1.
 BERTHOLD. 1886. *Studien über Protoplasmame-*
chanik. Leipzig.
 DETMER. 1882. *Eiweisszerfall*. *Ber. Deutsch. Bot.*
Ges., 10.
 LEPESCHKIN. 1910. *Z. Kenntn. Plasmamembran.*
Ber. Deutsch. Bot. Ges.
 —. 1911. *Struktur d. Protoplasmas*. *Ber. Deutsch.*
Bot. Ges.
 —. 1912. *Z. Kenntn. d. Todesursache*. *Ber.*
Deutsch. Bot. Ges.
 —. 1913. *Physiko-chem. Bau d. lebend. Sub-*
stanz. *Kolloidzeitschr.*
 —. 1923. *Constancy of living substance*. *Studies*
f. Labor. Plant Physiology, Charles Univ.
 Prague.

LEPESCHKIN. 1924. *Kolloidchemie d. Protoplasmas*.
 Springer, Berlin.
 —. 1924. *Ursache d. Hämolyse*. *Medd. K. Akad.*
Nobelinstitut. Stockholm.
 —. 1925. *Protoplasma d. Infusorien, Foramini-*
feren u. Radiolarien. *Biologia Generalis*.
 —. 1925. *Morpholog. Eigentümlichkeiten d.*
roten Blutkörperchen im Lichte d. Kolloid-
chemie. *Biologia Generalis*.
 —. 1926. *Chloroplasten v. Bryopsis*. *Ber.*
Deutsch. Bot. Ges.
 —. 1928. *Chemical and physical structure of*
protoplasm. *Science*, June.
 —. 1929. *Thermic effect of death*. *Journ.*
Gener. Physiol.
 —. 1930. *My opinion about protoplasm*. *Proto-*
plasma.
 —. 1930. *Thermic effect of death and hemoly-*
sis. *Am. J. Physiol.*, 95.
 PFLÜGER. 1873. *Physiologische Verbrennung d.*
lebenden Organismen. *Pflüger's Arch.*, 10.
 VERWORN. 1903. *Cited acc. to Allgemeine Phy-*
siologie, p. 633. VII. Aufl. 1922.





THE "CONCEPT OF ORGANISM" AND THE RELATION BETWEEN EMBRYOLOGY AND GENETICS

PART III

By J. H. WOODGER

University of London

PART II of this article (10) was devoted to a study of some of the postulates, assumptions, and order-systems upon which all inference in genetical and embryological science depends. It was pointed out that the whole biological realm could be regarded as exemplifying what is here called "hierarchical order." This means, roughly, that in this realm there are entities constituting systems with respect to relations having the formal properties of the relation which has been symbolized by R_H . The fundamental relation upon which all the rest depends is that between a given cell and the cell of which it is one of the immediate division products. It was symbolized by $R_H(d)$. Cells, therefore, are the entities constituting the *field* of this relation, and are divisible into three groups: (1) those belonging *only* to the *domain* of $R_H(d)$ (hence cells which do not divide); (2) those belonging *only* to the *converse domain* of $R_H^*(d)$ (hence zygotes which divide); and (3) those belonging to *both* the domain *and* the converse domain of $R_H(d)$ (i.e. all cells, except those which do not divide, and zygotes). Gametes belong to the first group but are distinguished from the rest by the fact that they also belong to and exhaust the converse domain of the second fundamental relation, namely, that between a zygote and each of the two gametes from which it is formed by fusion (R_f). Thus

three kinds of cells are distinguished in the above way: (i) zygotes (symbolized by o), i.e. cells belonging to the domain of R_f and the converse domain of $R_H(d)$; (ii) gametes (g), which belong to the converse domain of R_f and to the domain of $R_H(d)$; and (iii) all other cells, namely those which do not belong to the field of R_f . These will be called " α -cells." The only cells which do not satisfy the above definitions are gametes which do not unite and zygotes which do not divide, but as neither of these types are important from the present standpoint they can be neglected. Zygotes which do not divide are the only cells which do not belong to the field of $R_H(d)$.

Every cell which belongs to the field of $R_H(d)$ is a member of a *system* of cells standing in hierarchical order, and here called a division hierarchy (dW), the ordering relation being $R_H(d)$. In Part II it was shown how the powers of this relation determine certain important classes of cells. One of these was defined as "the class of cells consisting of all the contemporary descendants of a given zygote at moment m ." In Metazoa these cells are so related to one another as to constitute *components* of one organism. Together they constitute a level (the cell-level) in a *spatial* hierarchy (sW) in which there may be higher levels. Components (as contrasted with constituents) are of three principal kinds: (1) cellular

components of the first (P'), second (P''), or third (P'''), etc., orders; (2) "non-cellular" components, i.e. cells which are components (either c - or g -cells); and (3) cell-components of the first (p'), second (p''), or third (p'''), etc., orders, according to the degree to which analysis is carried. The spatial whole (sW) represents the entity " W " of the abstract definition of hierarchical order, and the corresponding relation, $R_H(s)$, is the relation of a given component of level L_n to the component of level L_{n-1} of which it is a component. Different spatial hierarchies (which in Metazoa may also be called "temporal slices" or "temporal parts" of ideally small temporal extent) of a given division hierarchy will be distinguished by subscript letters, thus: sW_n , sW_m , sW_x , etc. The sW_n (say) of dW_1 will be written " sW_n, dW_1 " (the inverted comma being read "of") to distinguish it from the corresponding slice of another similar division hierarchy dW_2 , which will accordingly be written " sW_n, dW_2 ."

The genetic hierarchical relation, $R_H(g)$, was defined as the relative product of the converse of $R_H^p(d)$ and the converse of R_f , when the converse domain of $R_H^p(d)$ is limited to zygotes, and its domain is limited to gametes. In this way we obtain a relation between zygotes, which thus constitute the field of $R_H(g)$. A genetic hierarchy with respect to a given zygote o_1 was then defined as the class of zygotes consisting of o_1 and all zygotes standing in $R_H^p(g)$ to o_1 . It was also shown how powers of this relation determine classes of zygotes which are precisely analogous to the corresponding classes determined by powers of the other hierarchical relations. The resemblances and differences between this and the other hierarchies were also pointed out. Having now sufficiently established these three exemplifications of the hierarchical rela-

tion (i.e., the ordering relation in a system of entities in hierarchical order) we can abandon the cumbersome symbols $R_H(d)$, $R_H(s)$, and $R_H(g)$, and substitute R_d , R_s and R_g respectively, with corresponding alterations for the powers of these relations.

Some explanation was given in Part II of the different kinds of *difference* which have to be considered in a causal analysis. We distinguished *manifest* difference (D_m), which is immediately observed, from *intrinsic* difference (D_i), which is assumed in accordance with the causal postulate. Intrinsic difference was also said to be of two kinds: either (1) *relational* difference (D_r), when the difference between two entities is regarded as being dependent upon a difference between two other entities in their (approximately) simultaneous environment; and (2) *specific* difference (D_s), for a difference between two entities which is not regarded as being dependent upon a difference between two other entities. The adjective "specific" will here be used exclusively in this sense, not in any special biological sense. It will be seen below that we have to discriminate between a number of quite distinct kinds of specific difference in biology which are frequently confused.

A few words must be added about "identity" and "non-difference." When we say " x is identical with y ," where x and y are organisms or parts of organisms, we may mean one of two things. (1) We may mean merely that " x " and " y " are two different symbols for one and the same entity. For this meaning I use the sign " $=$." (2) But more commonly we mean that x and y are two place-dates (see Part II, p. 444) with (ideally) the same intrinsic pattern, e.g. two (theoretically) "identical" twins. For this relation I shall use the symbol " I ," and shall

refer to it as "non-difference." Subscripts corresponding to D_i , D_s , D_m will also be used. Thus " $(o_1)I_s(o_2)$ " will mean "the zygote o_1 is not specifically different from the zygote o_2 ." We always assume (given "normal" conditions of perception) that D_m implies D_i , but of course we cannot say that I_m implies I_i (cf. Part II, p. 446).

Something must be said about the theory of comparison, although justice cannot be done to this difficult subject in a short space. We must to a very large extent follow the usual practice of relying on the reader's intuition to bridge over difficulties which have not yet been subjected to logical analysis. In the first place what is compared is always the manifest character (in the widest sense) correlated with the two entities. In biology we compare the manifest pattern correlated with one spatial whole (sW), or with a spatial part of that whole, with the manifest pattern correlated with another spatial whole, or with a *corresponding* spatial part of that other whole. There are then two distinct cases: (1) when the spatial wholes concerned belong to *different* division hierarchies (taxonomic biology), and (2) when they belong to the *same* division hierarchy (embryology). In the first case, not only must the spatial parts compared be "corresponding" or "homologous" parts (no one who wanted to compare two dogs would compare the tail of one with the head of the other), but the temporal parts or slices (sW) of the two division hierarchies compared must also be "corresponding" or "temporally homologous" parts. No one who wished to compare two different gramophone records of the same symphony would compare the first movement of one with the second movement of the other. He would compare "corresponding" movements. We should not say that one performance of a symphony gradually "comes

to resemble" another performance of the same symphony. But we often find in biological literature references to "that wonderful process" by which a fertilized ovum "comes to resemble" its parents. This is an instance of the way in which "problems" have been created by bad terminology and inadequate analysis. For it is evident that two division hierarchies which are related as parent to offspring resemble one another *throughout*, like the two performances of the same symphony. Zygote resembles zygote, gastrula resembles gastrula, and so on. Each successive slice as it is realized resembles the *corresponding* slice of the parental series.

We have the general term *color* to cover red and blue and green, etc., we have the general term *length* to embrace all the particular lengths, and similarly the term *weight* for the various particular weights. But there seems to be no term in general use for color *and* length *and* weight *and* . . . etc., so that it will be useful to use the word *determinable* for this purpose (see Johnson (5)). We can then say that in genetic experiments what is compared is the particular determinate character d_1 under the determinable δ of the spatial part μ of the slice sW_n of the division hierarchy dW_1 , with the particular determinate d_2 under the determinable δ of the spatial part μ of the slice sW_n of the division hierarchy dW_2 . We might, for example, be comparing a particular shade of gray under the determinable color of the skin of the adult rabbit *A*, with the particular shade of brown under the determinable color of the skin of the adult rabbit *B*. In each case the determinable, the spatial part, and the temporal slice must be "the same" although displayed in different division hierarchies. In embryological investigations the procedure is different, but the difference can only be made clear as we proceed.

II

Our next task is to make clear the different sorts of specific difference which are involved in biology. We must first state the basic theorems upon which all reasoning in embryology and genetics rests. In what follows "*dW*" will always mean a division hierarchy throughout its temporal extent, from the zygote up to the latest slice considered, and "*EdW*" will mean the environment of that division hierarchy throughout its extent up to the latest slice considered. For brevity we can write "*sW_n' dW₁*" for "the particular slice *n* of the division hierarchy 1," the inverted comma being read "of." Subscripts are merely distinguishing tags without any ordinal significance unless the contrary is stated. It must be remembered that we are not here concerned with the question how these theorems are applied in practice, but with what is ideally involved if *exact inferences* in regard to these topics are to be possible. We do not need to repeat the whole rigmarole about determinate characters, determinables, etc., but, taking this as now understood, we can simply state that two corresponding slices of two different division hierarchies are or are not *manifestly* different. Our first theorem can therefore be stated as follows:

(1) If

$$(sW_n' dW_1) D_n (sW_n' dW_2).$$

then (by the causal postulate and definition of *D_i*)

$$(sW_n' dW_1) D_i (sW_n' dW_2).$$

Hence (by definition of *D_s*):

(2) If

$$(sW_n' dW_1) D_i (sW_n' dW_2)$$

and

$$(EsW_n' dW_1) I (EsW_n' dW_2)$$

then

$$(sW_n' dW_1) D_s (sW_n' dW_2).$$

This, then, is one sort of specific difference, a specific difference, namely, between two corresponding slices of two division hierarchies, which slices have the same environment. But suppose the environments of the two division hierarchies were non-different *throughout*, i.e., from the zygote *o* up to *sW_n*, then if *sW_x* is *any* slice prior to *sW_n* we shall have the following theorem:

(3) If

$$(sW_n' dW_1) D_s (sW_n' dW_2)$$

and

$$(EdW_1) I (EdW_2)$$

then

$$(sW_x' dW_1) D_s (sW_x' dW_2).$$

Moreover, since the zygote is a slice of a division hierarchy (the "first" slice) it is a value of *sW_x*, and we have as a corollary:

(4) If

$$(sW_n' dW_1) D_s (sW_n' dW_2)$$

and

$$(EdW_1) I (EdW_2)$$

then

$$(odW_1) D_s (odW_2).$$

These two theorems are obviously ordinarily assumed in genetic interpretations. If two eggs are incubated in the same incubator and if the birds that hatch out are manifestly different, few geneticists would hesitate to assume that the zygotes had been specifically different. It might not even be recognized as an assumption, but it is evident that these theorems are simply consequences of the a priori causal postulate.

Now it is plain that in theorems (3) and (4) we have introduced much more than was involved in "specific difference" as we find it in theorem (2). In the latter case we have a difference between two spatial hierarchies which involved no

explicit reference either to the earlier slices of the division hierarchies to which they belong, or to the environments of the latter. Theorems (3) and (4), on the other hand, clearly state that there is a specific difference which is pervasive *throughout* the division hierarchies up to sW_n , so long as the environments have been non-different throughout. It will not, therefore, be surprising to find that the interpretation of "specific difference" in the two cases is different. But before this is discussed we must consider some embryological theorems. Let sW_n and sW_m be two slices of the *same* dW , sW_m being later than sW_n , then:

(5) If

$$(sW_n) D_m (sW_m)$$

then (by the causal postulate)

$$(sW_n) D_i (sW_m).$$

(6) If

$$(sW_n) D_i (sW_m)$$

and EdW has been constant or uniform throughout up to sW_m , then

$$(sW_n) D_s (sW_m).$$

This evidently follows from the definition of D_s , the causal postulate, and the hypothesis that EdW has been uniform (a condition which is presumably closely approximated to in amniotes for considerable periods). Thus theorem (6) *again* introduces specific difference, and we now have to consider its interpretation in relation to the others.

When we say that two corresponding slices of two *different* division hierarchies are specifically different in the sense of theorems (3) and (4) we usually mean that they belong to different races, or species, or genera, etc., but when we say that two slices of the *same* hierarchy are specifically

different in the sense of theorem (6) do we mean that they are specifically different in the *same* sense? Do we suppose, for example, that a human zygote is specifically different from an adult man in the *same* sense in which a human zygote would be regarded as specifically different from an amoeba? Do we suppose that a human zygote belongs to a different race, species, or genus, etc., from an adult man? I take it that we do not and that, in consequence, specific difference means something quite different in the two cases. Even those people (if there are any left) who regard all zygotes as amoebae with their pseudopodia on the first rung of the ladder by which each "climbs up its own ancestral tree," will be compelled to make this distinction. They will be compelled, that is to say, if they admit the causal postulate, to assume some difference between the several alleged "amoebae" in accordance with which they climb up *different* trees.

There is another way in which we might bring out this point. Let odW_1 and sW_n be two slices of dW_1 , namely the zygote and some later slice, such that $(odW_1) D_s (sW_n, dW_1)$ in the sense of theorem (6). Let odW_2 and sW_n, dW_2 be corresponding slices of dW_2 , such that $(odW_2) D_s (sW_n, dW_2)$ in the same sense. Let dW_1 and dW_2 both have the same environment up to sW_n , and be specifically different in the sense of theorem (3). Now since $(odW_1) D_s (odW_2)$ we also have $(sW_n, dW_1) D_s (sW_n, dW_2)$. For since $(odW_1) D_s (odW_2)$ and $(EdW_1) I (EdW_2)$ we cannot have $(sW_n, dW_1) I (sW_n, dW_2)$. Because if $(sW_n, dW_1) I (sW_n, dW_2)$ when $(odW_1) D_s (odW_2)$, then (by the causal postulate) either: $(sW_n, dW_1) D_s (odW_1)$, or $(sW_n, dW_2) D_s (odW_2)$. But embryologically we *do* have $(sW_n, dW_1) D_s (odW_1)$, etc. Hence D_s means something different in embryology from what it does in genetics. In other words

the specific difference between a human zygote and a monkey zygote is a *different sort* of specific difference from the difference between a human zygote and an adult man, although both are specific differences in the sense defined in Part II. (These two sorts of difference seem to have been confused in the doctrine of recapitulation). We must therefore seek for an interpretation of the two kinds of specific difference which will make this distinction clear, and we require to use a corresponding difference of language. I shall call the difference between two specifically different division hierarchies a *genetic* difference (D_g), and the difference between two specifically different slices of the *same* hierarchy will be called a *developmental* difference (D_d).

Now since, as was pointed out above, the specific difference of theorem (3) is one which is pervasive *throughout* the two division hierarchies, so long as their environments are non-different, its interpretation can, it seems, only be sought in something which is common to *all* slices. And one thing which we can say about every slice is (by definition, see Part II) that it consists of a class of cells (in the case of the zygote-class this is a class with only one member). Consequently the hypothesis suggests itself that when we say that two division hierarchies are genetically different, or specifically different in the sense of theorem (3), we are really making an assertion about the *kind of cells* occurring in the two hierarchies, i.e. we are saying that all the cells of the one hierarchy belong to one kind of cell, and all the cells of the other hierarchy belong to another and different kind of cell, or that any cell of the one hierarchy is specifically different from any cell of the other, in the same sense in which the zygote of the one is (by hypothesis or inference as in theorem (4)) specifically

different from the zygote of the other. And since every cell in a division hierarchy stands in a relation which is some power of R_d to the zygote of that hierarchy, this is equivalent to saying that if c_1 and c_2 are any two c -cells (belonging to dW_1 and dW_2 respectively, odW_1 and odW_2 being the two corresponding zygotes) then, if $(odW_1)D_s(odW_2)$, and if $(c_1)R_d^p(odW_1)$ and $(c_2)R_d^p(odW_2)$, then $(c_1)D_s(c_2)$. But if, on the other hand, c_1 and c_2 are such that $(c_1, c_2)R_d^p(odW_1)$, i.e. both belong to the *same* division hierarchy, then $(c_1)I_s(c_2)$. Let this be provisionally adopted as an interpretation of D_s in the sense of theorem (3). It will also serve as a definition of genetic difference as that expression is here used, i.e. (setting out the definition in full): " $(k_1)D_g(k_2)$ " is to mean: " k_1 and k_2 are two cells such that $(k_1)R_d^p(odW_1)$ and $(k_2)R_d^p(odW_2)$, and $sW_n'dW_1$ and $sW_n'dW_2$ are two corresponding slices of dW_1 and dW_2 respectively and such that $(sW_n'dW_1)D_m(sW_n'dW_2)$ and $(EdW_1)I(EdW_2)$."

We can leave any further discussion of the above hypothesis for the present in order to turn to the interpretation of the second kind of specific difference, i.e. developmental difference, the definition of which may be stated as follows: If sW_n and sW_m are two slices of the same division hierarchy, sW_n being earlier than sW_m , then " $(sW_n)D_d(sW_m)$ " is to mean: " $(sW_n)D_s(sW_m)$ and EdW has been uniform up to sW_m ." For the interpretation of this kind of specific difference we have to recall what was said in Part II about the interpretation of specific difference between two organized entities. It was there pointed out that we ordinarily assume that if two such entities are specifically different this is because they differ: (1) in the *number* of their parts, and/or (2) in the *relations* in which those parts stand to one another, and/or (3) in the

kinds of parts into which they are analysable. Applying this postulate (which we shall refer to as the Postulate of Analytical Interpretation) to the case of $D_d(sW_n, sW_m)$ we can proceed as follows: sW_n and sW_m are both (by definition of sW) analysable into cells, consequently they will differ in (1) the number of cells, and/or (2) the relations between the cells, and/or (3) the kinds of cells, into which they are analysable. Now, in the course of development, by the mere continuation of division (or spatial repetition of the cell-pattern), we have an increase in the number of the cells, and this same process, coupled with movements of cells, or of cellular components, will yield differences in the relations in which the cells stand to one another (in the spatial hierarchy), whilst, in later slices especially, we soon begin to find manifest differences between the cells, from which we infer (by the causal postulate) that such cells are *intrinsically* different, and if these differences are not purely relational, we shall have cells within the hierarchy which are *specifically* different, i.e. different kinds of cells. Thus all the three possibilities offered by the Postulate of Analytical Interpretation appear, in general, to be realized in developmental difference. But the admission that there may be specifically different cells in the *same* division hierarchy appears to conflict with our previous assumption that if c_1 and c_2 are any two c -cells of a given dW then $(c_1)I_s(c_2)$. But this we called a genetic difference or non-difference, and it may be possible for two cells in the same dW to be specifically non-different in *this* sense, and yet be specifically different in some *other* sense. It seems, then, that we shall have to distinguish yet another kind of specific difference, and again a difference between cells. That is to say: there may be two different sorts of sorts of cells. And, if you are classifying cells

according to their genetic sort (as above defined) then all the c -cells of a given dW may be of the same sort, or genetically non-different, whereas, if you are classifying them according to some *other* mode of classification the cells of a given dW may *not* be all of the same sort. If this were the case there would be nothing contradictory in our procedure.

It was pointed out in Part I (9) p. 12, that there are two ways in which cells which are specifically different may arise in a division hierarchy (although the expression "specifically different" was not used in Part I). These two ways are (1) differentiating division, and (2) histological elaboration. If a cell divides in such a way that, in consequence of the division, the cells are specifically different (as appears to be the case in the "mosaic eggs") we have differentiating division. But if the two resulting cells are not specifically different but only *become* so *after* division, in consequence of their different organic relations in the spatial hierarchies, then the two cells will be said to have undergone histological elaboration. For example, numerous experiments have now shown that the sort of histological elaboration a cell or its cell-descendants will undergo depends, in a given division hierarchy, on its relations to certain other cells, or cellular components. Maximow (6) gives an example from hematology. He believes that the large lymphocyte-like cells of both the lymph nodes and the bone-marrow are not specifically different, but that the differences manifest in their cell-descendants are a consequence of their different relations in lymph nodes and bone-marrow respectively. He writes:

Using the method of tissue culture, Maximow attempted artificially to change the external conditions for the lymphocytes by explanting them into a medium which would as nearly as possible correspond to the medium normally surrounding the lymphoid

stem cells in the myeloid tissue and might induce them to display their latent granulopoietic potencies. In fragments of lymphoid tissue, developing in vitro in a mixture of blood plasma and bone marrow extract, he observed proliferation of large lymphocytes with differentiation into special and eosinophilic myelocytes and megacaryocytes.

In this way, then, we may have specifically different cells in the same division hierarchy although they may not be specifically different in the sense of being *genetically* different. We therefore require a name for this new kind of specific difference between cells belonging to the same division hierarchy. I shall call it *histological* difference (D_h), but it is not to be understood in a narrow, static or "anatomical" sense, but in a wide sense to include dynamic or "physiological" differences as well. For the present we may define this difference as follows: If c_1 and c_2 are two cells such that $(c_1)D_s(c_2)$, and o is a zygote such that $(c_1, c_2)R_d^p(o)$, then $(c_1)D_h(c_2)$.

Another convenient way of expressing this difference between two sorts of sorts of cells is by saying that cells which are *not* genetically different belong to the same "G-type," and cells which are not histologically different belong to the same "H-type." And our assumption so far is (provisionally) that two c -cells belonging to the same division hierarchy are of the same G-type, but need not be of the same H-type. If they are manifestly different they will probably be specifically different, and so of different H-type, e.g. a muscle-cell and a nerve-cell of the same division hierarchy.

It is clear from the above that genetics is primarily concerned with the study of cells from the standpoint of their G-type, not with "characters." The latter are only an index of whether the cells of two division hierarchies, having the same environment, are or are not specifically

(and hence genetically) different. The aim of the geneticist is to avoid the necessity of referring to the environment by keeping it the same for both of the division hierarchies compared. But of course this does not mean that the environment is "of no importance." If it were so no such precaution would be necessary. Embryology, on the other hand, is concerned with the process of passage from one sW to another in the same dW , and, in so far as it can occur in a uniform environment, this is an *immanent* process, and this again (as here understood) does not mean that the environment can be ignored, but only that *if* the process occurs in a temporally uniform environment, then the changes in the former cannot be interpreted as resulting from a one-one correlation with changes in the latter, since, by hypothesis, there are none.

There is still another case of "specific difference" not yet dealt with—that, namely, in theorem (2), in which we have $(sW_n' dW_1)D_s(sW_n' dW_2)$ when $(EsW_n' dW_1)I(EsW_n' dW_2)$. I shall say, in this case, that the two corresponding slices of the two division hierarchies are *taxonomically* different (D_t). This term may not be free from objections, but so long as the exact sense in which it is here used is remembered, no confusion need result from its use, and it seems better to use this term than to invent a totally new one. Taxonomic difference in this sense, then, is simply an actual specific difference between corresponding slices of *two* division hierarchies, and is thus distinguished from developmental difference, which is an actual specific difference between two slices of the *same* dW . It is to be interpreted in the same way as the latter by an appeal to the Postulate of Analytical Interpretation. Thus, if two such slices are taxonomically different they will differ (1) in the *number* of cells into which they are analysable,

and/or (2) in the *relations* in which the cells stand to one another, and/or (3) in the *kinds* of cells into which they are analysable. In actual practice, of course, we do not usually possess the requisite data to enable us to express taxonomic difference in this way. We express it more often in terms of the determinate characters which the two slices exhibit under various determinables, or in terms of the possession or lack of various cellular components or constituents (manifest difference), although theoretically these should ultimately be expressible in terms of (1), (2), or (3) above (or combinations of them), if we adopt the causal postulate and that of analytical interpretation. In regard to (3) we can now see that, in view of our assumption that there are two kinds of kinds of cells, there will be two possibilities with respect to *G*-type. The cells of the two spatial hierarchies compared will either belong to the *same* or to two *different G*-types. If the former is the case then, assuming the casual postulate, it will follow that the taxonomic difference will be wholly the result of environmental differences (i.e. differences in the environments of dW_1 and dW_2) even although the environments of the *actual slices compared* are (by hypothesis) not different. We could say that in that case the two taxonomically different spatial hierarchies are also *environmentally* different. Similarly, if we knew that the zygotes of the two division hierarchies concerned were of *different G*-type (i.e., genetically different), and if their environments had been non-different throughout, then we could say that the taxonomic difference between the two corresponding slices compared was wholly the result of the genetic difference between their cells. Thus two taxonomically different spatial hierarchies may be (1) wholly environmentally different and not genetically different; (2) geneti-

cally different but not environmentally different, or (3) "mixed" i.e. belonging to division hierarchies which have had different environments and whose cells are of different *G*-type. In actual practice the last possibility will, presumably, be that most often realized, although it is the aim of experiment to have either (1) or (2), and not (3), realized. But it must always be remembered that our fundamental theorems are a priori and "ideal" in the same sense in which Newton's first law of motion is a priori and "ideal." They can be neither proved nor disproved by an appeal to experiment. They serve rather to determine the form and limits of the "logical space" in which we propose to let our thoughts move in regard to these matters. They are adopted because of their success in guiding experiment and in systematizing our data.

The results of the foregoing analysis of specific difference can be summarized in a table which shows what entities constitute the field of these relations of difference, and thus determine their range of significant application.

Relation	Field
D_o	Specifically different cells of different division hierarchies.
D_h	Specifically different cells of the same division hierarchy.
D_a	Specifically different slices of the same division hierarchy.
D_t	Specifically different corresponding slices of different division hierarchies.

Note: Although " D_o " is strictly a difference between *cells* it is also convenient to speak of genetically different dW 's, sW 's, or cell-cones. This will mean, therefore, that *any* *c*-cell of the one dW (sW or cell-cone) is genetically different from *any* *c*-cell of the other dW (sW or cell-cone).

We can now pass on to consider briefly how the above analysis can be applied to the clarification of the problems involved in

- (1) The interpretation of the developmental process.
- (2) The relation between G-type difference and taxonomic difference.
- (3) The interpretation of histological difference.
- (4) The interpretation of genetic difference.
- (5) The distribution of G-type differences among the members of a genetic hierarchy.

III

We can begin with the first of these questions. The interpretation of development requires an analysis of the process in which developmentally different spatial hierarchies in the same division hierarchy are successively realized. Our definitions of differentiating division and histological elaboration (see above) provide us with four theoretically possible types of division hierarchy according to the occurrence or non-occurrence in them of either or both of these processes:

- (1) Division hierarchies in which neither differentiating division, nor histological elaboration occurs.
- (2) Division hierarchies in which differentiating division, but no histological elaboration, occurs.
- (3) Division hierarchies in which histological elaboration, but no differentiating division, occurs.
- (4) Division hierarchies in which *both* differentiating division *and* histological elaboration occur.

If type (1) were realized in nature it is plain that two slices of such a division hierarchy could not differ from one another in the *kinds* of their cells, apart from differences arising merely from different environmental contingencies. They would be "equipotential systems" in Driesch's sense. Such a state of affairs conflicts so clearly with what we observe

in the development of most organisms that we seem to have but three alternatives: (i) to deny that type (1) occurs in nature, (ii) to suppose that it occurs and then either (a) to reject the causal postulate and that of analytical interpretation, or (b) to adopt Driesch's view of development, which is equivalent to retaining the causal postulate whilst rejecting the postulate of analytical interpretation. And since it is a question of choice of a priori postulates it is clearly useless to suppose that such questions can be settled by an appeal to experiments, as Driesch does. Unless, then, we are prepared to revise our usual postulates in natural science, we are driven to assume that division hierarchies of type (1) do not occur in nature. I said in Part I (p. 21) that it is "important to know whether there *really are* equipotential systems in the organic realm," but it seems clear to me now that, *so far as whole organisms are concerned*, we are driven to assume that there are no such things, so long as we adhere to our present postulates.

If type (2) occurred in nature we should have to say that all differences between different slices of the same division hierarchy were a consequence of differentiating divisions, (apart, of course, from differences resulting from environmental changes). Such cases may occur in nature, but transplantation experiments clearly exclude the possibility of regarding all division hierarchies as of this type. Moreover, it is difficult to see how, if all histological elaboration is rigorously excluded, it would be possible to have gametes in later slices of the hierarchy, although the difficulty is not in principle greater in regard to gametes than in regard to muscle or nerve cells, except that gametes are required to have, in general, the same properties as those which went to the formation of the zygote from which the hierarchy was generated.

If type (3) occurred in nature it would

again be extremely difficult to interpret development with out present postulates. We should then have to suppose that *all* differences between cells and cellular components (except differences in number of cells in different slices) were, in origin, *purely* relational. This would mean either that they resulted from purely contingent environmental differences between the cells, or we should have to suppose that they can arise in precisely similar cells simply in consequence of the different relations in which they come to stand in the course of cleavage. There are plenty of experiments which definitely rule out this type of division hierarchy as one of wide spread occurrence. This leaves us with type (4).

Type (4) offers a compromise between the two extremes of (2) and (3). Those cases in which a typical division hierarchy can be generated from a single isolated cleavage cell lead us to assume that non-differentiating divisions occur at least up to the level in which the cell in question occurs. In other cases ("mosaic eggs"), in which this is not so, we are driven to assume differentiating divisions from the beginning. But in such cases, for reasons given in Part I, we cannot expect differentiating divisions alone, without histological elaboration, to fulfil all the requirements of an interpretation of development in the later slices. Consequently the most reasonable view seems to be that division hierarchies of type (4) are those realized in nature, and this assumption will be adopted in what follows. But it must be remembered that we are referring only to differentiating divisions with respect to *H*-type, all divisions being assumed (for the present) to be non-differentiating with respect to *G*-type. Weismann does not appear to have made a distinction of this kind, and his scheme is not therefore easily comparable with the present one.

He assumed that all divisions in the cell-ancestry of the gametes were of type (1), (3) or (4) in Fig. 3, Part II (p. 452), and that all other divisions were of type (2).

We must go back now and review the above considerations in their relation to other developmental processes. In Part I it was pointed out that we could regard development as the outcome of *three* major processes of elaboration, namely:

- (1) Cell-elaboration.
- (2) Histological elaboration.
- (3) The elaboration of *cellular* components.

(1) Cell-elaboration was described in Part II as being achieved through the spatial repetition of an intrinsic cell-pattern. The *cell*-pattern is spatially repeated whenever a cell divides into two *cells* (as contrasted, say, with two *half*-cells), but, on the assumption we have made regarding *G*-type, if a cell c_1 is genetically different from another cell c_2 , then, when c_1 divides into c_1' and c_1'' , we shall have $(c_1', c_1'')I_a(c_1)$ and $(c_1', c_1'')D_a(c_2)$. There is, therefore, spatial repetition not merely of a "cell-pattern in general," but of a *specific* cell-pattern. When a monkey-zygote divides it does not merely divide into two cells, but into two *monkey*-cells, and so on. But since, with respect to *H*-type, we are assuming that a cell may undergo differentiating division, the cell-pattern will, it seems, be such that it contains elements which are *not* spatially repeated in all divisions, but are capable of being differentially distributed among the two cells into which a given *c*-cell may divide. We might thus be led to suppose that there were two fundamentally different kinds of cell-part, and it may be that only those which are capable of spatial repetition are components (as defined in Part II).

- (2) In histological elaboration some-

thing happens in a cell which has not previously happened in cells ancestral to it. This is most evidently the case when there are manifest differences between cells indicating the presence of special cell-constituents. But the expression is here used in a wide sense, leaving open the question whether special cell-components or constituents are involved or not. Relational difference (as defined in Part II) may play a great part in the early stages of development, and all difference arising from histological elaboration *begins* as relational difference.

(3) The elaboration of cellular-components is presumably achieved through a combination of processes (1) and (2). As we have seen, spatial repetition of a specific cell-pattern alone would not yield cellular components. But, combined with differentiating division, provided the planes of division were suitable, it would yield a system of cells analysable into ordered classes of cells according to their different *H*-types. But to carry this through the whole of development would involve (except in the case of the simplest organisms) a prodigious preformation. We are therefore driven to assume that histological elaboration also occurs, so that our first cell-classes resulting from cell-elaboration and differentiating divisions become divided into sub-classes in consequence of histological elaborations occurring in some of the cells and not in others—this difference between them resulting from differences in their relation to other components in the spatial hierarchy. But we require a better way of expressing the relation between a state of affairs in a given *sW* and the state of affairs in earlier slices. Let us first write down a list of what appear to be the fundamental *cell* processes involved, and then we shall see what other notions are required to enable us to deal with the elaboration of

cellular components. Such a list is especially important when we come to consider the connexion between *G*-type differences and differences in developmental processes as displayed in different division hierarchies.

Cell-Processes

- (i) Basic metabolic processes, (including:
- (ii) *Maintenance* of specific cell-pattern),
- (iii) Spatial *repetition* by division of specific cell-pattern (with or without:
- (iv) Differentiating division, with respect to *H*-type),
- (v) Histological elaboration,
- (vi) Movement.

Now it seems clear that we cannot describe development exclusively in terms of such cell-processes because some of the occurrences we have to describe involve properties which (as was pointed out in Part I, p. 19) are properties not of single cells but of systems of cells. Two systems of cells are of special importance, namely: (1) cell-cones (defined in Part II), and (2) what I shall call cell-series, and by this I simply mean the ordered class of cells constituted by a given cell plus all the cells standing in conv. R_d^p to it, i.e. the cell-ancestors of a given cell together with that cell itself. There is one other notion required for the present, namely that of a *developmental route*, which may be defined as follows: Let $c_1, c_2, c_3, \dots o$, constitute a cell-series of which c_1 is the representative in a slice sW_n and o is the first member (being the zygote of the division hierarchy to which c_1 belongs). Then let R_1, R_2, R_3, \dots represent the organic relations in which these members of the cell-series (except o) stand in the successive temporal parts of the dW , and let $E_1, E_2, E_3, \dots E_o$, represent the environment of these same successive temporal parts or slices of the

division hierarchy. Then by the developmental route of the cell c_1 I mean the whole set of organic relations and environmental relations of the members of the cell-series to which c_1 belongs.

Now consider any cell c in some late slice of a division hierarchy. Let the symbol $(C.G.H.)$ represent (i) that it is a cell, i.e. has the cell-pattern, (ii) that it belongs to a certain special class of cells (G -type) the members of which are distinguished in some way from all other cells, and (iii) that it also belongs to a certain H -type, i.e. to a certain special sub-class within the wider class indicated by its G -type. We now have to consider upon what the G - and H -type of c depend. So far the assumption has been made that the G -type of c depends only upon the G -type of the zygote o to which it stands in some power of R_d . And since this is equally true of every cell of this division hierarchy, c will not be distinguished from its neighbors in G -type. The question of its H -type is more complicated. We can conceive the H -type of c to be possibly dependent upon (1) its cell-ancestry, and/or (2) its developmental route. That the H -type of c depends on its cell-ancestry follows at once from the admission of differentiating division, since it is evident that its H -type will depend on the differentiating divisions that have occurred in its cell-ancestry. That the H -type of c depends on its developmental route seems to be equally clear from numerous transplantation experiments which consist in allowing cell-series to be generated in a developmental route different from that in which they would have been generated had it not been for the experimental interference.

It will be noted that $(C.G.H.)$ cannot represent a possible state of affairs until we indicate how the cell in question is related to other things. Thus $(C.G.H.)E$ would represent a zygote, a detached

gamete or a protozoon (or protist); $(C.G.H.)R_s(sW)E$ would indicate that the cell belonged to a spatial hierarchy with no cellular components (although it does not indicate its precise place in the system); $(C.G.H.)R_s(P)R_s(sW)E$ would represent a cell belonging to a given cellular component P of an organism possessing cellular components, and so on for cellular components of higher orders. These further complications cannot be neglected when the relational properties of cells (as defined in Part I) are in question.

The following quotations from Weismann (8) will serve to throw into relief the differences between his fundamental assumptions and the modern ones:

the fate of the cells is determined by forces situated within them, and not by external influences. a certain cell in a subsequent embryonic stage does not give rise to a nerve-, a muscle-, or an epithelial-cell because it happens to be so situated as to be influenced by certain other cells in one way or another, but because it contains special determinants for nerve-, muscle-, or epithelial-cells.

For these assumptions I substitute (from the standpoint of the concept of organism) the following:

the future history of a given cell c which is a component in a spatial hierarchy, depends on (1) its G -type, (2) its H -type, (3) its organic relations to the rest of the organism, including its relation to the component (if any) of which it is a component, and (4) the external environment.

To which may be added in further elucidation:

the G -type of c depends on the G -type of the zygote to which it stands in R_d^p . Its H -type depends on (1) the occurrence of differentiating divisions in one or more of the members of its cell-ancestry, and/or on (2) its developmental route.

Thus the modern view is a good deal more complicated than Weismann's (and this is a good sign), but it is none the less the outcome of a consistent application of the two postulates of causation and of ana-

lytical interpretation to the data yielded by modern experiments. It should be noted that no reference has been made to chromosomes or even to nuclei. To translate "G-type difference" into "chromosome difference" is simply to make a further hypothetical application of the postulate of analytical interpretation. But the above reasoning is entirely independent of any such hypothesis, and would still hold if we knew nothing about nuclei. Any one, therefore, who adopts the above two postulates, and the few elementary data and assumptions that have been invoked, is compelled to adopt the rest, provided the reasoning has been correct, whatever view he may take regarding the chromosome hypothesis. This will be clear from a reference to the definitions which have been progressively built up from the beginning of Part II.

It is always much easier to think in terms of cells than in terms of cell-systems, but in dealing with the elaboration of cellular components one is compelled to deal with cell-systems. This is facilitated by the use of the notion of the cell-cone. Considerations of space forbid any detailed discussion here, but a few important points may be illustrated. Suppose we are comparing two slices of the same division hierarchy during the developmental period, call them sW_n and sW_m (sW_n being earlier than sW_m). Then it is evident that there will be cell-cones having their apical cells in sW_n and their basal cells in sW_m , the latter consisting of the classes of cells (in sW_m) which are the contemporary descendants of the apical cells belonging to sW_n . Thus sW_m is analysable into classes of cells consisting of such "bases" of cell-cones. Moreover, the apical cells of such cones in sW_n will also fall into classes which are the basal cells of cones having *their* apical cells in still earlier slices. Now such cell-cones

will be either homogeneous or non-homogeneous, a homogeneous cell-cone being defined as one in which no differentiating divisions take place. But such a cell-cone could become non-homogeneous in the sense of containing cells of different H -type if some of its members come into such relation with other cones that they undergo histological elaborations which do not occur in the rest of the cone to which they belong. Suppose, for example, that all the epidermis cells of one side of the head in a frog in a certain early slice sW_n belong to the same homogeneous cell-cone, and that all the cells of the outer wall of the optic vesicle of that side all belong to another homogeneous cell-cone. Then a small sub-class of the former class gives rise to a number of cones whose basal cells in a later slice sW_m undergo histological elaboration into lens-cells. And we know that *which*, in some animals, of the cells of the former class of epidermal cells is selected to start these lens-cell-cones depends on which are organically related in a particular way to the optic vesicle cells. Thus a considerable part in development would appear to be played by a combination of (1) the generation of different cell-cones following differentiating division, (2) the diversification of such cones by different histological elaborations in some members of them in accordance with their different organic relations, followed by (3) the elaboration of more cells yielding more homogeneous cones consisting of cells of the newly elaborated H -type. An important type of histological elaboration from this point of view is that which expresses itself in increased or decreased rate of cell-elaboration. One cell-cone may differ from another in the time interval which separates the members of the cell-series into which it is analysable. This may be expressed more precisely as follows: Let c_1 and c_1' be the apical cells of the two

cell-cones compared, and let c_4, c_3, c_2, c_1 and c_4', c_3', c_2', c_1' be the two cell-series to which they belong, and which belong to the two cones. Then if the temporal stretch between c_4 and c_1 is shorter than that between c_4' and c_1' , and if this difference holds good also for the other cell-series into which the two cones are analysable, then the rate of division in the cone generated from c_1 would be greater than that in the cone generated from c_1' . These, then, are some points in the interpretation of the elaboration of cellular components, but they scarcely touch the surface of the problem. Among contemporary ideas in embryology the Field Theory of Gurwitsch (3) and his school seems to be the only one which shows any promise of dealing at all adequately with this, the most difficult aspect of development.

We can now say something about the second of the questions drawn up at the end of Section II above. This was the question: How are differences of G -type related to taxonomic differences? We have seen that, if (\mathcal{W}_n, dW_1) and (\mathcal{W}_n, dW_2) are the two slices compared and found to be taxonomically different from one another, and if we can assume that $(EdW_1)I(EdW_2)$, then we shall be dealing with a case of taxonomic difference which is wholly the outcome of a difference of G -type between the cells of the two division hierarchies compared. We have also seen that the taxonomic difference between the two slices will be a difference (assuming the postulate of analytical interpretation) of (1) number of cells, and/or (2) relations between the cells (e.g. differences between cellular components), and/or (3) the kinds of differentiating divisions and histological elaborations exhibited by the cells of the two spatial hierarchies. Now since in each case the number of cells, relations between the cells, and the histo-

logical elaborations, etc., which the cells exhibit are the outcome of the developmental processes we have already discussed, it follows that the differences between the two spatial hierarchies under consideration will be wholly the outcome of differences in the developmental process in the two cases, and these differences in turn will (assuming the causal postulate) be the consequence of the differences in the G -type of the cells of the two hierarchies. Suppose the manifest difference between the two spatial hierarchies is only one of skin color, then the developmental process which is different in the two cases will be that of the histological elaborations in the skin-cells in the two cases. Suppose it is a difference in shape or number of some cellular component, then it will be a question of difference in the complex processes involved in the elaboration of the cellular component concerned, thus involving relations between cells. It is in this case that it is most difficult to understand how G -type difference is correlated with taxonomic difference. Suppose we have to do with a difference in size of part or whole, then it will be a question of the rate of division in corresponding cell-cones in the two cases. Thus although, as we have seen, the history of a given cell may depend not only upon its G -type, but also on (1) its cell-ancestry, (2) its developmental route, (3) its relations in the spatial hierarchy to which it belongs, and (4) the environment (E) of that hierarchy, although this is the case, yet, if we have two division hierarchies with the same environment but different G -type, this difference of G -type may result in such differences in the early developmental processes as to produce differences in (1) the cell-ancestry, (2) the developmental route, and hence (3) the relations in the spatial hierarchy, of a cell in a much later slice. Consequently differences of G -

type may have either a direct or a remote effect on the behavior of a given cell in corresponding slices of two genetically different division hierarchies in the same environment.

We can now discuss the interpretation of a certain type of experiment which has important bearings on the foregoing problem. I refer to those experiments in which an embryonic part is transplanted to another organism of different species

the properties of the genetic hierarchy to which dW_1 belongs) we expect to furnish cell-descendants in a later slice sW_m which will constitute a cellular component P_1 characterised by the particular determinate character d_1 under the determinable δ , Fig. 1A. Let k_1 be a corresponding group of cells in sW_n dW_2 , expected to give origin to a corresponding component P_1 , but characterised by a different determinate character d_2 under the determinable δ_1 in

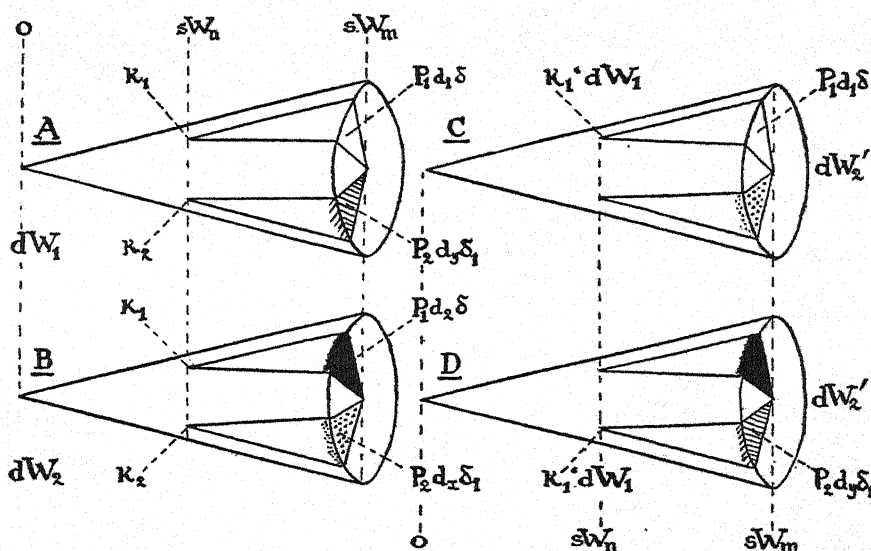


FIG. 1. DIAGRAM OF EXPERIMENTS OF THE TYPE DISCUSSED IN THE TEXT

A four-dimensional division hierarchy is represented by a three-dimensional cone. A plane of the cone perpendicular to its vertical axis represents in two dimensions the three-dimensional spatial organism conceived in abstraction from time (sW). The apex of the cone represents the zygote. The wedge $k_1 - P_1$ represents the system of cell-cones generated from the cell-group k_1 and resulting in the establishment of the cellular component P_1 . For further explanation see text.

and to a site different from that which it normally occupies in the organism to which it belongs, and is then found to develop "ortsgemäss" while at the same time retaining its "species specificity." Such experiments have been thought to conflict with current genetical theories. I think it can be shown that this is not the case, (see Part I, p. 18). Suppose we have two genetically different division hierarchies dW_1 and dW_2 . Let k_1 be a group of cells in the slice sW_n of dW_1 which (from a knowledge of

sW_m dW_2 , Fig. 1B. Let k_2 be another group of cells of sW_n dW_2 giving origin to a totally different component P_2 characterised by d_x under determinable δ_1 ; and let k_2 of sW_n dW_1 be a corresponding cell-group yielding P_2 (homologous with P_2 of dW_2) but characterised by d_y under determinable δ_1 . Now suppose we find that k_1 , when transplanted to the site of k_1 in sW_n of another division hierarchy dW_2' of the same G-type as dW_2 , yields P_1 characterised by d_1 under δ , instead of d_2 ,

Fig. 1C. Then we can say, using the causal formula:

$$D_m(P_1' dW_2', P_1' dW_2) \cdot C.$$

$$D(G\text{-type } k_1' dW_1, G\text{-type } k_1' dW_2)$$

i.e. the difference between the P-components of the two division hierarchies is causally correlated with the difference in the G-type of the cells derived from dW_1 and those of dW_2' . The transplanted cells, having the same G-type as that of the other cells of the division hierarchy whence they came, have given origin to cell-cones in which the cells have undergone histological elaborations of the same type as they would have done on the original site. This also assumes that the G-type is not changed by transplantation, and that the organic relations or developmental routes of the P-cells of dW_2' were not sufficiently different from those of the P-cells of dW_1 to alter the histological elaborations of the cells derived from the transplanted k_1 cells.

But suppose k_1 of dW_1 had been transplanted to the site of k_2 in $sW_n' dW_2'$, and had furnished cells constituting the component P_2 in $sW_m' dW_2'$, but characterized by d_y under determinable δ_1 , Fig. 1D. Then, comparing, $sW_m' dW_2'$ with $sW_m' dW_2$, we should again have:

$$D_m(P_2' dW_2', P_2' dW_2) \cdot C.$$

$$D(G\text{-type } k_1' dW_1, G\text{-type } k_2' dW_2')$$

The difference in the determinate characters manifested by the two corresponding parts would again be correlated with the difference in the G-type of the cells involved. But if we compare dW_2' with dW_1 we have to account for the difference between the behavior of the cell-descendants of k_1 in the two cases, and this can only be correlated with differences between the organic relations of the cell-cones involved in the two cases. If we let K_1

stand for the whole slab of cell-cones involved in the development of P_1 in dW_1 and K_2 for the corresponding slab of cell-cones in dW_2' , and if R_1 and R_2 represent the set of organic relations or developmental routes in the two cases (E being supposed to be the same for both) then we have:

$$D(K_1, K_2) \cdot C \cdot D(R_1, R_2)$$

No G-type difference is involved, since the cells of K_2 and of K_1 have the same G-type. And since P_2 in dW_2' and P_2 in dW_1 are homologous cellular components, present in *both* division hierarchies, there is no difference in them *as* components, e.g. they may both be legs, or skin, or neural tube, or what not. It is only in their determinates under various determinables, e.g. color, that they differ. Consequently *as cellular components which "correspond"* in the two division hierarchies there is no $D(P_2' dW_1, P_2' dW_2')$ with which we need to find a correlated pair of G-type differences. So long as cells come from division hierarchies which are capable of elaborating a cellular component of the P_2 -type there is nothing surprising in their being able to furnish such a component in a different species or genus which is capable of elaborating such a component, so long as the transplanted cells have not already undergone their definitive histological elaboration. For with respect to P_2 -elaboration there is no reason to suppose that the two division hierarchies are genetically different, or, in other words, such genetic difference as may exist between them does not affect the processes concerned in the elaboration of a P_2 -component as such, i.e. does not affect the early phases of its elaboration, but only the later ones in which histological elaboration occurs in its cells. Thus it is sometimes said that such experiments show that some processes are "species

specific" and others not, and that the latter are not dependent upon the chromosomes. But, in such cases as the above the "other processes" are not processes in which the two division hierarchies concerned differ, consequently it is not surprising that the result of transplantation is such as we observe. The organizer formed by the blastoporic lip, for example, is said not to be "species specific," but is this not simply because all the "species" upon which it can be transplanted have this type of developmental process in common? We can express this by saying that there is no difference of *G*-type involved so far as this process is concerned, whatever may be the truth about the chromosomes. But when we consider the particular determinate character d_1 exhibited by P_2 in dW_2' as contrasted with P_2 in the "normal" dW_2 , then we do have another correlated pair of different entities, namely the k_1 cells from dW_1 and the different (in *G*-type) k_2 cells in dW_2 . Fig. 1 will make these points clear.

We can summarize the chief features of the developmental process in the following general terms: Development is the realization of a pattern in time (like a tune) by the spatial repetition of a specific *cell*-pattern with the consequent elaboration of a *cellular* pattern, constituted by cells in organic relation. This cellular pattern becomes diversified by the elaboration of cellular *sub*-patterns in consequence of the elaboration of *different* cells, either by differentiating divisions, or by histological elaboration in accordance with the different organizing relations set up in consequence of previous differentiating divisions. The pattern of the whole, and of its cellular components, continually changes through the generation of new cell-cones, thus yielding more and more elements of pattern capable of further diversification in the sub-patterns. De-

velopment is *dependent* throughout on the environment but, in so far as it occurs in a temporally uniform environment, the *temporal* pattern of a division hierarchy (i.e. its temporal diversification) is not dependent upon environmental *changes*. Development is, therefore, to this extent and in this sense an immanent process.

Before concluding this section a few points of difference between division hierarchies in metazoa and protozoa may be mentioned in passing. The fundamental difference depends, of course, on the fact that, save in respect of its cellularity, a given member of a protozoan division hierarchy is comparable not with a cell but with a temporal slice (δW) of a metazoan division hierarchy. That is to say it does not stand in a relation R_s to any other organic entity. Consequently such a protozoan cell cannot undergo histological elaborations in accordance with its R_s relations since there are none, and there will be no such thing as "*H*-type." As regards *G*-type the same principles hold in both cases. But, although there is no such thing as *H*-type difference, one member of a protozoan division hierarchy may differ from another, even although it does not differ in *G*-type. Such differences will correspond to the contingent relational or specific differences between different division hierarchies in metazoa which result from different environments (environmental taxonomic differences).

IV

The second, fourth and fifth questions raised at the end of Section II are obviously related, and together cover a whole group of problems. They involve all the topics usually embraced under Classification, Phylogeny and Mendelism. Something must first be said about classification and the analysis of classificatory propositions. If our previous reasoning has been correct,

and our basic assumptions suitably chosen, a taxonomic difference between two corresponding slices of two division hierarchies which is wholly the outcome of a genetic difference between the two zygotes, will be at bottom a *cell* difference, i.e. a difference in the *G*-type of the cells of the two organisms. Accordingly a rational classification would be based on this. In actual fact, of course, the traditional classification has not been based on this for the simple reason that we know next to nothing about it. Instead, it has been based on a comparison of the manifest sense-patterns correlated with the two organisms, and this alone tells us nothing about the *G*-type of their cells. In our present method of classification the various taxonomic groups are defined by sets of propositional functions stating the "diagnostic characters." (A propositional function is, roughly, a function which becomes a proposition when some definite entity is substituted for its argument. Thus " x has non-nucleated red blood-corpuscles" is a propositional function which defines the class "mammalia.") This procedure corresponds to a classification of chemical entities in terms only of their manifest characters, without reference to their "properties" (e.g. solubility, vapor density, specific gravity, precipitation reactions, etc.) and is obviously beset with great difficulties. In the first place it makes no explicit reference to the environment, although there must be a tacit assumption that the latter has been "normal." A systematist who was given a "cycloplan" *Fundulus* (and knew nothing about the experiment with magnesium) would either put it aside as "abnormal" or place it in a totally different taxonomic group from that of "normal" specimens, although, in a classification based upon the *G*-type of their cells, two such fishes might be placed in the same group.⁴ In the

second place, this method usually makes no explicit reference to the temporal extension and diversification of organisms (division hierarchies), and the common restriction to the adult may lead to some strange misunderstandings.

What do we mean by assertions of the type " x is an *S*," where x is some short temporal slice of a division hierarchy (metazoan), and *S* is the name of some taxonomic group, some order, genus, species or variety, etc.? We usually mean that x is one of the values satisfying the various propositional functions which constitute the definition of *S*. But x may not satisfy a single one of these functions, and may yet be called an *S*. We say that all chordates have a notochord, but no chordate animal has a notochord before it reaches the "gastrula" stage, and no adult mammal has a notochord. Yet we do not for this reason deny the title "chordate" to *Amphioxus* while it is a blastula, nor do we deny it to an adult rabbit. We are thus compelled to introduce the question of temporal diversification, and " x is a chordate" may then (it seems) mean either of two things: (1) It may mean "the visual pattern correlated here and now with x exhibits the features recognized as 'notochord,'" or it may mean (2) " x is a slice of a division hierarchy some *past* slice of which exhibited a notochord." This would meet the case of the adult rabbit, but it would not do for the *Amphioxus* blastula, nor the rabbit before the primitive streak stage. We might then try again and say that " x is a chordate" means (3) " x is a slice of a division hierarchy some slice of which *will have* a notochord." But this is to make an assertion about the future about which we know nothing, not about x . There may never be a future slice of the x division hierarchy to have a notochord; x may be trodden on, or dropped into a fixing fluid.

Our classificatory propositions are not hypothetical assertions about the *future* of organisms. We therefore require an interpretation of " x is an S " which will show it to be an assertion about x itself, *whatever slice* of the division hierarchy x may be. And clearly, on the basis of our previous analysis, such an interpretation will be provided if we say that " x is an S " is an assertion about the G -type of the cells of x . There will thus be two meanings of propositions of the type " x is an S ." They will mean either (1) " x here and now satisfies the defining functions of the group S ," or, (2) " x here and now is a cell (i.e. a zygote), or is analysable into cells, having a certain G -type, namely, the G -type characteristic of the cells of all division hierarchies which satisfy the defining functions of the group S in a certain environment." Consequently, when we say " x is an S " in this second sense we are not saying anything about one particular slice of a division hierarchy, but something which may be said about *any* slice. Moreover, on the assumption that the G -type is constant, this assertion makes no reference to the particular environment of the division hierarchy concerned.

The fundamental difference between these two meanings lies in the fact that the first makes an explicit reference to a particular slice (although it may be a "long" slice in the case of the adult) whereas the second, as we have said, is under no such restriction. In consequence of this the first meaning involves the *notion of development*, and the second does not. In terms of this analysis we can now state why it is that we feel that, in regard to a hen's egg in an incubator, *if* it develops at all what hatches out of it will be far more like a fowl than like any other organism, whereas we should be quite prepared to admit that even in the best of incubators it might not

develop *at all*. It is because "hatching out like a fowl" depends on the successful accomplishment of the developmental process, which we find by experience to be liable to environmental contingencies. But "being a fowl" in the second of the above meanings of " x is an S " does not involve the developmental process at all. In *this* sense what is in the egg at the start is as much a fowl as what hatches out of it at the end, and experience has taught us that the G -type of cells (to adopt the terminology of this paper) is relatively constant, and remarkably immune from ordinary environmental contingencies. To emphasize this point it will be convenient to call the first of the above meanings of " x is an S " the *developmental meaning*, and the second meaning the *genetic meaning*, or non-temporal meaning, since it does not (we are assuming) share in the temporal diversification of the division hierarchy.

Lack of space precludes the possibility of giving here detailed examples of the way in which the foregoing analysis enables us to avoid many of the perplexities still current in attempts to bring embryological and genetical data into relation to one another, but a consideration of the following passage from Dürken (2) will illustrate some important points:

Although there may be no essential difference between racial, specific and even generic characters, yet there is certainly one between the properties by which during development one of the higher organisms becomes a bilateral structure, a fish, reptile, bird or mammal, in comparison with those which cause the color of the hair or of the eyes, the form and length of the body, tail or ears.

It is not easy to know what precisely is intended by an "essential difference" in this passage, but I do not think that such a distinction as is here suggested either need or can be made. Dürken also speaks of "essential" and "inessential" *characters*, and if this simply means that one can get

on quite well with a long or a short nose, but not without a nose at all, then it is easy to understand what is meant. But this is a different matter from saying that there is an essential difference between the developmental process through which one comes to achieve a nose, and that in virtue of which one achieves a long or a short one. I should say that the former was chiefly a question of the elaboration of a cellular component or constituent and was very complicated, whereas the second would chiefly be a question of the rate of division in certain of the cell-cones involved in that elaboration. But as far as dependence upon G-type of the cells is concerned there seems to be no need to make any sharp distinction between them, although it is this which Dürken has in mind in the context of the above passage. It occurs to me that one reason for the belief that some such important distinction is necessary is the failure to distinguish the two meanings of " x is an S," together with some lingering misunderstandings left by the phylogenetic discussions of the last century. If we speak of the process "by which during development one of the higher organisms becomes a fish" we can only be speaking of the *developmental* sense of " x is (or becomes) a fish." We are then referring to those developmental processes through which the particular components and constituents are elaborated in virtue of which x satisfies the defining functions of "fish." But there is never a time in which x is not a fish in the second or genetic sense, and hence no need for anything to "cause" it to become one. When we turn to the developmental processes through which the eyes become green, the hair brown, the body, tail or ears long, we do not appear to have to deal with a situation which in principle is in any fundamental way different from the former. If x is a fish in

the genetic sense, so it will be a green-eyed fish, or a brown-eyed fish, or a ... etc.-eyed fish in the genetic sense, although the division hierarchy to which it belongs may or may not later realize a slice which is a green-eyed fish in the developmental or first sense—since this depends on environmental contingencies. Some Neo-Lamarckians say that blueness of eyes is an "inherited" character and sunburnt skin an "acquired" one. But "being blue-eyed" and "being sunburnt" either in the developmental or in the genetic sense are not fundamentally different (if the foregoing analysis is adopted). The only difference in this case is that if (at present) a human division hierarchy is to be generated *at all*, up to the slice which exhibits an eye, this can only happen in an environment which, to a high degree of probability, will also ensure that the eye is blue, if the hierarchy is genetically blue. But it may easily go through its whole temporal extent without encountering an environment requisite for it to be developmentally sunburnt, even although it is genetically sunburnt! In order to be developmentally blue-eyed it is necessary to be genetically blue-eyed *and* to encounter a blue-eye-realizing environment. And the same is true *mutatis mutandis* of becoming developmentally sunburnt. That this is not so shocking as it looks will be seen from a reference to the genetic meaning of " x is an S."

There is, however, one obvious difference between the so-called "essential characters" and the "inessential characters." One cannot have a green eye if one does not have an eye, and one cannot have a long nose if one does not have a nose. But, on the other hand, one cannot have *merely* an eye first of *no* color, or a nose first of *no* length, and then proceed to stick "characters" on to these nondescript parts like tickets on the goods in a shop window. The fact is that parts such as

"eye" or "nose," like the whole organism itself, are four-dimensional temporally extended things, and their temporal boundaries are vague. We speak of the first beginnings of such parts as eye or nose rudiments, leg and tail buds, etc., and these have length and color, and other determinables just as the fully developed parts have. When the color or length, etc., of such a part is spoken of it is the color, etc., of the *fully* developed part that is usually meant. Consequently such characters are manifested relatively late in development, and are regarded as something superficial which *might not* be there, and hence are called inessential. Whereas the *parts*, the later slices of which they characterise, have their first slices early in development and come to be regarded as "essential," because if anything went wrong with them the consequences for later slices of the division hierarchy would be serious. The fact that the developmental process is such that the late slices of a part can only be formed on the basis of the earlier ones does not seem to be any reason for supposing any fundamental difference to exist between the developmental processes concerned.

This brings us to the celebrated *Biogenetische Grundgesetz*. (How fond the Victorians were of *Gesetze*! Any generalization, however vague, was dignified by the name of "Law".) In this generalization a parallel is drawn between three sets of data, and this parallelism is based on the formal resemblance of various types of *inclusion relation* which occur in the three sets of data. There is first the set of taxonomic data, with the various taxonomic groups one within another. This is the logical relation of inclusion between classes. Then there are embryological data of the type to which we have alluded, some parts, namely, have a greater temporal extent than others, which are parts

of them. This is a relation of spatio-temporal inclusion. Finally we have certain phylogenetic relations founded upon palaeontological data. For example, the temporal extent of fishes is greater than that of amphibians, that of amphibians greater than that of reptiles, and so on. This is a relation of inclusion of durations. We can illustrate this a little more fully as follows; (Fig. 2).

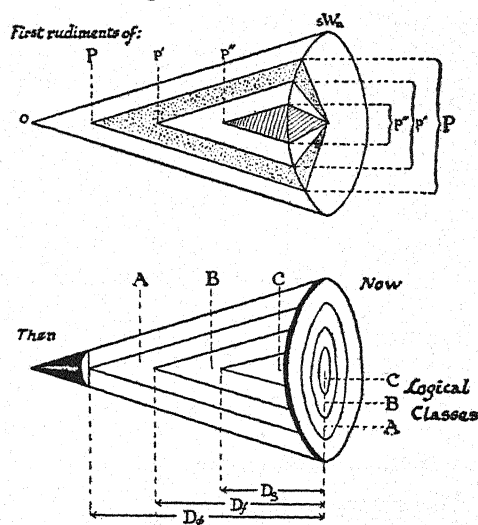


FIG. 2. DIAGRAM ILLUSTRATING THE "BIOGENETIC LAW"

The upper figure represents a division hierarchy in the same manner as in Fig. 1, showing the successive appearance of the sub-components of the cellular component *P*. The lower figure illustrates the time of evolutionary appearance of taxonomic groups of the kind discussed in the text, and the resulting inclusion-relation of the (logical) classes of organisms. For further explanation see text.

(1) *Taxonomic data*. Let ϕx stand for some propositional function which sufficiently defines some animal phylum. Similarly let $f x$ define a class of that phylum, $g x$ an order of that class, $F x$ a family of that order, and so on until we get to the smallest taxonomic group in which all the members have precisely the same *G*-type (this may be a group with only one member). Now in general we find that the number of organisms satisfying

on quite well with a long or a short nose, but not without a nose at all, then it is easy to understand what is meant. But this is a different matter from saying that there is an essential difference between the developmental process through which one comes to achieve a nose, and that in virtue of which one achieves a long or a short one. I should say that the former was chiefly a question of the elaboration of a cellular component or constituent and was very complicated, whereas the second would chiefly be a question of the rate of division in certain of the cell-cones involved in that elaboration. But as far as dependence upon G-type of the cells is concerned there seems to be no need to make any sharp distinction between them, although it is this which Dürken has in mind in the context of the above passage. It occurs to me that one reason for the belief that some such important distinction is necessary is the failure to distinguish the two meanings of " x is an S ," together with some lingering misunderstandings left by the phylogenetic discussions of the last century. If we speak of the process "by which during development one of the higher organisms becomes a fish" we can only be speaking of the *developmental* sense of " x is (or becomes) a fish." We are then referring to those developmental processes through which the particular components and constituents are elaborated in virtue of which x satisfies the defining functions of "fish." But there is never a time in which x is not a fish in the second or genetic sense, and hence no need for anything to "cause" it to become one. When we turn to the developmental processes through which the eyes become green, the hair brown, the body, tail or ears long, we do not appear to have to deal with a situation which in principle is in any fundamental way different from the former. If x is a fish in

the genetic sense, so it will be a green-eyed fish, or a brown-eyed fish, or a ... etc.-eyed fish in the genetic sense, although the division hierarchy to which it belongs may or may not later realize a slice which is a green-eyed fish in the developmental or first sense—since this depends on environmental contingencies. Some Neo-Lamarckians say that blueness of eyes is an "inherited" character and sunburnt skin an "acquired" one. But "being blue-eyed" and "being sunburnt" either in the developmental or in the genetic sense are not fundamentally different (if the foregoing analysis is adopted). The only difference in this case is that if (at present) a human division hierarchy is to be generated *at all*, up to the slice which exhibits an eye, this can only happen in an environment which, to a high degree of probability, will also ensure that the eye is blue, if the hierarchy is genetically blue. But it may easily go through its whole temporal extent without encountering an environment requisite for it to be developmentally sunburnt, even although it is genetically sunburnt! In order to be developmentally blue-eyed it is necessary to be genetically blue-eyed *and* to encounter a blue-eye-realizing environment. And the same is true *mutatis mutandis* of becoming developmentally sunburnt. That this is not so shocking as it looks will be seen from a reference to the genetic meaning of " x is an S ."

There is, however, one obvious difference between the so-called "essential characters" and the "inessential characters." One cannot have a green eye if one does not have an eye, and one cannot have a long nose if one does not have a nose. But, on the other hand, one cannot have *merely* an eye first of *no* color, or a nose first of *no* length, and then proceed to stick "characters" on to these nondescript parts like tickets on the goods in a shop window. The fact is that parts such as

"eye," or "nose," like the whole organism itself, are four-dimensional temporally extended things, and their temporal boundaries are vague. We speak of the first beginnings of such parts as eye or nose rudiments, leg and tail buds, etc., and these have length and color, and other determinables just as the fully developed parts have. When the color or length, etc., of such a part is spoken of it is the color, etc., of the *fully* developed part that is usually meant. Consequently such characters are manifested relatively late in development, and are regarded as something superficial which *might not* be there, and hence are called inessential. Whereas the *parts*, the later slices of which they characterise, have their first slices early in development and come to be regarded as "essential," because if anything went wrong with them the consequences for later slices of the division hierarchy would be serious. The fact that the developmental process is such that the late slices of a part can only be formed on the basis of the earlier ones does not seem to be any reason for supposing any fundamental difference to exist between the developmental *processes* concerned.

This brings us to the celebrated *Bio-genetische Grundgesetz*. (How fond the Victorians were of *Gesetze*! Any generalization, however vague, was dignified by the name of "Law".) In this generalization a parallel is drawn between three sets of data, and this parallelism is based on the formal resemblance of various types of *inclusion relation* which occur in the three sets of data. There is first the set of taxonomic data, with the various taxonomic groups one within another. This is the logical relation of inclusion between classes. Then there are embryological data of the type to which we have alluded, some parts, namely, have a greater temporal extent than others, which are parts

of them. This is a relation of spatio-temporal inclusion. Finally we have certain phylogenetic relations founded upon palaeontological data. For example, the temporal extent of fishes is greater than that of amphibians, that of amphibians greater than that of reptiles, and so on. This is a relation of inclusion of durations. We can illustrate this a little more fully as follows; (Fig. 2).

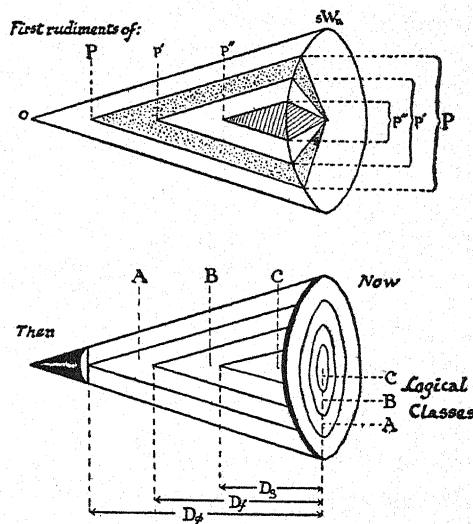


FIG. 2. DIAGRAM ILLUSTRATING THE "BIOGENETIC LAW"

The upper figure represents a division hierarchy in the same manner as in Fig. 1, showing the successive appearance of the sub-components of the cellular component P. The lower figure illustrates the time of evolutionary appearance of taxonomic groups of the kind discussed in the text, and the resulting inclusion-relation of the (logical) classes of organisms. For further explanation see text.

(1) *Taxonomic data*. Let ϕx stand for some propositional function which sufficiently defines some animal phylum. Similarly let $f x$ define a class of that phylum, $g x$ an order of that class, $F x$ a family of that order, and so on until we get to the smallest taxonomic group in which all the members have precisely the same G-type (this may be a group with only one member). Now in general we find that the number of organisms satisfying

ϕx is greater than that of those satisfying fx . The number of organisms satisfying fx is usually greater than that of those satisfying gx , and so on. Moreover every organism which satisfies gx also satisfies fx , and every one which satisfies fx also satisfies ϕx . It is because the class (in the logical sense of "class") determined by gx is included in the class determined by fx that the number of organisms satisfying fx is greater than the number satisfying gx . And so on for other groups. It is because the defining character of fx is thus possessed by more organisms than that of gx that the former is called a "more general" character than the latter.

(2) *Embryological data.* Suppose the function ϕx is " x has P ," where P is some part possessed by all adult organisms satisfying ϕx , and by no others. And suppose P is one of those parts discussed above which extend over a comparatively large temporal slab of the division hierarchy, their first appearance being early in development. Suppose fx is " x has p " where p is a part which is a part of P . Similarly, let p' be a part of p possessed by all organisms satisfying gx . (For example, P might be such a part as a paired appendage in vertebrates, p' might be the distal part or hand, and p'' one of the digits.) Then it is clear that P will appear first in development, p' next, and p'' next. The first beginnings of P will be common to the embryos of all organisms satisfying ϕx , p' will be common to the embryos of all organisms satisfying fx , and p'' only common to those satisfying gx . If now we call the group of organisms satisfying ϕx A , that satisfying fx B , and that satisfying gx C , we have the following parallelism between the inclusion relation of these groups, and the spatio-temporal overlapping of the parts and sub-parts:

(C) is included in (B), which is included in (A)

(p'') is preceded by (p'), which is preceded by (P)

It is the combination of these two sets of propositions which underlies von Baer's rules:

1. In development from the egg the general characters appear before the special characters.
2. From the more general characters the less general and finally the special characters are developed.

(3) *Phylogenetic data.* From palaeontological information, coupled with the assumptions of the doctrine of evolution, we might be able to assert the following:

Put D_ϕ for "the duration in which there have existed organisms satisfying ϕx ."

Put D_f for "the duration in which there have existed organisms satisfying fx ."

Put D_g for "the duration in which there have existed organisms satisfying gx ."

Then, parallel with our taxonomic and embryological inclusions we may have:

(D_g) is included in (D_f), which is included in (D_ϕ). Moreover, if, in accordance with the demands of the doctrine of evolution, we consider all the zygotes of organisms satisfying ϕx , from the beginning of D_ϕ to the present, they will constitute a "zygote-cone" analysable into n sub-cones one of which constitutes the zygotes of all organisms satisfying fx from beginning of D_f , and this will be analysable into m sub-sub-cones, one of which is constituted by the zygotes of all organisms satisfying gx , from the beginning of D_g . These relations are represented diagrammatically in the accompanying Fig. 2. It is evident that "recapitulation" results from the fact that p'' is a part of p' , and p' a part of P . We cannot have p' until we already have the first slices of P , nor p'' until we already have the first slices of p' . All organisms satisfying ϕx will have the

first beginnings of P , but the fully developed P will not be the same in all organisms satisfying ϕx because only some have p' , namely those satisfying ϕx , and this group does not exhaust the group determined by ϕx , and so on for the smaller groups. But it seems clear that p' is not simply planted on top of an *adult* condition of P , nor p'' on an adult p' . If two organisms belonging to different orders differ in their p'' -like parts they will diverge in their developmental processes before the definitive condition of p'' is reached.

Two organisms are said to be related because they both satisfy ϕx . They both satisfy ϕx because their developmental slices up to a certain slice sW_n have a part which is an early slice of P . They both have such a slice because (presumably) the G -type of their cells is *not different with respect to this particular developmental event*. And their G -types resemble one another to this extent because (according to the doctrine of evolution) they belong to genetic hierarchies which, if they could be traced back far enough, would be found to overlap completely in their earlier levels. Thus corresponding to the taxonomic hierarchy we seem to require a hierarchy of G -types.

This, then, is the basis of the doctrine of recapitulation. But it is only exemplified in regard to parts which have the above overlapping nature. It is not exemplified by parts that are analysable into cells which do not have contemporary descendants in later slices, such as foetal membranes. The doctrine does not provide a "causal explanation" of development as an experimental embryologist would understand that expression, but only in the sense in which the doings of Guy Fawkes in the seventeenth century provide a "causal explanation" of the letting off of fire-works by little boys in England on the night of the fifth of

November in each year. In so far as it combines the third of the above sets of parallel propositions with the first two it is a historical rather than a causal explanation.

G. R. de Beer (1) has recently pointed out various ways in which (theoretically) a change in the G -type of a genetic succession of zygotes might lead to changes in the developmental processes in the division hierarchies generated from them. In terms of our three fundamental developmental processes we might state some of these as follows: Changes in

A. Cell-elaboration

(1) In an early slice

(a) With, and (b) without, disturbance of later slices.

(2) In a late slice.

B. Histological elaboration

(1) In an early slice

(a) With, and (b) without, disturbance of later slices.

(2) In a late slice.

C. Cellular component elaboration

(1) In an early slice

(a) With, and (b) without, disturbance of later slices.

(2) In a late slice.

It is evident that the earlier the slice affected the more drastic the consequences for later slices, provided the part in question is analysable into cells, which have cell-descendants in later slices. In general one would expect the consequences of such changes to be lethal. That is perhaps why (if they occur at all) their consequences are so rarely observed. In so far as later slices *only* are affected we shall have recapitulation (or repetition in de Beer's terminology) in parts of the type which exhibit such a process (as explained above).

Reverting once more to purely embryological matters we can make a brief review of one of Driesch's arguments in the light of the foregoing discussions. Driesch knows perfectly well that there can be no such thing as an empirical "proof" of vitalism. But he supposes that the terms "vitalism" and "mechanism" stand for two perfectly clear and definite doctrines which (i) mutually exclude one another, and (ii) between them exhaust all possibilities. Consequently he supposes that if one can be *disproved* the other is thereby established. I think it can easily be shown that these assumptions are by no means justified, but let us examine one of Driesch's most powerful arguments, which may be stated (I hope sufficiently accurately) as follows:

- (1) No natural entity can increase its degree of multiplicity "of itself."
- (2) Harmonious equipotential systems are natural entities in which the degree of multiplicity is increased but not in consequence of environmental occurrences.
- (3) Consequently in such systems there must be some "agency at work" which is "responsible" for this increase in multiplicity.
- (4) There are some embryos in nature which are harmonious equipotential systems.
- (5) Therefore in some embryos there are "agencies at work" through which their multiplicity is increased.

If any of these premises can be denied the argument collapses. I have already pointed out the difficulties of establishing proposition (4) empirically, because our current a priori postulates would lead us to deny that embryos, as wholes, can be equipotential systems, but let us leave this and consider the first proposition. Driesch regards this as an unshakable

dogma. But the following considerations suggest that, if the developing organism is conceived under the "concept of organism," it is not so inevitable as it seems to be at first sight. We have seen that an organized entity having components standing in internal organizing relations will have its degree of multiplicity increased if (i) the *number* of its components is increased, (ii) if the complexity of the *relations* in which those components stand to one another is increased, and (iii) if the *intrinsic patterns* of the components become different from one another (yielding intrinsically different components in the whole). Now in the generation of a division hierarchy in Metazoa we appear to have: (a) increase in the number of components by spatial repetition of the specific cell-pattern of the first member (the zygote); (b) increase in complexity of relations as more members appear; and (c) the becoming different of the components either by differentiating divisions or by histological elaboration, and, in consequence of this, the elaboration of components of a higher order (cellular components). Thus granted (i) the possibility of spatial repetition of a pattern, and (ii) the possibility of differentiating division and histological elaboration, and (iii) that, apart from these primary processes, there is no need to appeal to "agents" of *any* kind, and Driesch's argument is undermined, and the old puzzle of "preformation" and epigenesis" largely evaporates. If we do not need to invoke "entelechies" for the interpretation of cell-division this alone will suffice in principle, because even this process will yield an increase in multiplicity in succeeding slices of the division hierarchy. Neither the "preformationists" nor the "epigeneticists" knew anything of spatial repetition of pattern or of histological elaboration, since such processes occur only in living cells, and there was

therefore nothing in the experience of the early embryologists to suggest that such things occurred. These considerations illustrate the dangers of framing biological theories on ideas borrowed from outside the data of biology. From the point of view of the analysis of developmental processes given above there is no need to regard the zygote as a mystery-bag of "potencies" which, at their appointed hour, proceed to blossom out into the "characters" which they are said to be "for." We require to conceive any given cell as exhibiting one or more of the six fundamental cell-processes described in Section III above, in accordance with (1) its *G*-type (2) its *H*-type, (3) its relations in the spatial hierarchy, and (4) the environment of the latter. All these are among the "factors" of development, and all are liable to environmental contingencies in varying degrees, (1) being the most constant, and the only one which persists unchanged (usually) throughout development.

I do not wish to give the impression that the developmental process is simple; we are obviously only at the beginning of understanding it. I have already emphasized the special difficulties of dealing with the elaboration of cellular components. But I do suggest that the above analysis helps to remove some of the *obstacles* to an understanding of development which have been created by notions bequeathed to us by the older embryologists.

V

Little space remains for a discussion of the logic of Mendelism. Its chief importance lies in its bearing on the question of how we are to conceive "*G*-type" of cells. The fact that, from the union of different pairs of gametes from the *same* two division hierarchies (which are not genetically different) two or more *genetically different*

kinds of zygotes may result, *compels* us (when coupled with the causal postulate) to admit the occurrence of *differentiating division with respect to G-type* in some cell or cells which are ancestral to such gametes, and this contradicts our fundamental assumption that the divisions in a division hierarchy are non-differentiating with respect to *G*-type. This difficulty is removed when the division is assumed to occur (as it is on cytological grounds) in a *c*-cell which stands in conv. R_d^2 to a given tetrad of gametes. This assumption leaves the foregoing arguments, as far as development is concerned, entirely unaffected.

It is possible to state the Mendelian results in cases where different characters under *one* determinable are involved, in terms of different or non-different gametes, without saying anything "absolute" about them. But when we consider cases involving two or more determinables the situation becomes more complicated because we have to assume that a given gamete may be either singly or doubly different (in the case of two determinables) from another, and it is difficult then to interpret the resulting ratios without invoking the postulate of analytical interpretation, and thus assuming that the gametes are analysable into cell-components which are different or non-different as the case may require. We are thus committed to a "particulate view" and this has been objected to by some biologists. But such objections appear to rest on a failure to distinguish between a particulate theory from the standpoint of genetics and a particulate theory from the standpoint of embryology. Such objections are valid enough against the particulate theory of Weismann, but this theory did not itself discriminate between the requirements of genetics and those of embryology, whereas the modern particulate theory is a purely genetical theory. This is clearly recog-

nized by T. H. Morgan (7). The "particulate view" presents no difficulties to the "concept of organism." We have already seen that this concept *requires* that the organism should be analysable into a hierarchy of components, with the emphasis as much on the hierarchy as on the components. If the organizing relations are given equal weight with the components it is difficult to see what objections can be raised to so-called "particulate" theories. For, in any case, if once *cells* as components are admitted you have already admitted that the organism is in some sense "particulate," and it then seems arbitrary to draw the line below the cell-level.

I have postponed any reference to Mendelism and its consequences to the end because I wished to show how very largely the main features of our current genetical theory are really independent of it, and owe their present form to considerations of a much more general and elementary nature. I have tried to analyse out the principal postulates, assumptions, and empirical data upon which they rest. From this analysis we can see that anyone who wishes to oppose the predominant theory in genetics begins at the wrong end if he begins by attacking the chromosome theory, because the predominant theory is logically independent of the chromosome hypothesis, and its main features are even logically independent of Mendelism, as will now be clear. In consequence of this an opponent who begins at the wrong end may very easily find himself denying something which is a necessary deduction from premises which, in any other context, he would freely admit. I hope my analysis may go some way towards avoiding unnecessary disputes which rest on a failure to understand this point. The proper place for a critic to direct his attacks is at the beginning, namely, at the causal postulate and the postulate of analytical inter-

pretation, and this is a very difficult thing to do, although even a priori postulates should not be regarded as eternally fixed and unalterable. Our attitude towards them, at least, has changed in the course of history, even in the brief span during which human beings have indulged in thinking.

The controversy from which we began in Part II—the question of the "importance" to be "ascribed" to "environment" and "heredity"—should now appear in a clearer light. Is there any sense in asking how many centimeters of a man's nose are "due to heredity" and how many are "due to environment?" Is it not like asking how much of the volume of a gas is "due to" pressure and how much "due to" temperature? This can hardly be what people really have in mind when they raise such questions. Only with regard to two corresponding slices of two division hierarchies could we say, assuming that they had the same environment throughout, if they were manifestly different, that they were taxonomically different, and that this was wholly the consequence of a genetic difference between their zygotes. Or, if we assume that the zygotes were not genetically different we could say that the taxonomic difference was wholly the outcome of environmental difference. But clearly, the developmental processes in each, through which the taxonomic difference of the two slices compared is realized, are in both cases *dependent throughout* on the contemporary environment. We can contrast the two views which H. S. Jennings (4) discusses in the little book referred to in Part II. Jennings describes the view he is opposed to as follows:

Every individual, therefore, came into the world with his characters fixed and determined. His whole outfit of characteristics was provided for him at the start; what he should be was pre-ordained; predestination, in the present world, was an actual fact. Environ-

ment might prevent or permit the hereditary characters to develop; it could do nothing more.

And the view to which Jennings subscribes is stated as follows:

It is not true that what an organism shall become is determined, fore-ordained, when he gets his supply of chemicals or genes in the germ cells, as the popular writers on eugenics would have us believe. The same set of genes may produce many different results, depending on the conditions under which it operates. True it is that there are limits to this; that from one set of genes under a given environment may come a result that no environment can produce from another set. But this is a matter of limitation, not of fixed and final determination; it leaves open many alternative paths.

Now it is perfectly plain from these two passages that the whole dispute rests on a failure to discriminate between the two meanings of propositions of the type of " x is an S " as discussed in Section IV above. The first passage is obviously concerned with " x is an S " only in the *genetic* sense. Only in this sense can we say that what x "is" is "fixed and determined" at the start. If taken quite literally the first passage would lead to ridiculous consequences. It would mean that a man could have either a particular length of nose, according to the G -type of his cells, or, in cases where the environment "prevented" this, he would have *no nose at all!* And if this were the case we should expect to see many more people going about with holes in their heads or flat patches of skin in the place of a nose than we actually do. This view is so obviously silly that the people who hold it (if they are correctly reported) can hardly mean what they say. There is, however, one thing to be said in justice to the "popular writers on eugenics," namely, that if the view attributed to them above is correct, then the *things they say* about eugenics will *also* be "fixed and determined from the start" and cannot be attributed to defective education, but

simply to the peculiarities of their own "supply of chemicals."

Thus we can only say that an organism's characters are "fixed and determined" if we can say that the environmental contingencies which it will encounter as each successive slice is realized are fixed and determined. But even if this were the case we could not tell what the characters of future slices would be from a knowledge, however perfect, of the properties of the zygote alone. We should also have to know the laws of the environmental contingencies which each slice is to encounter, and also the laws governing the organism's response to those contingencies according to the slice of the hierarchy which happens to be realized when it encounters them. And of course we cannot speak of the organism as "having its whole outfit of characters provided for him at the start." The zygote has only the characters appropriate to it as such, and each later slice has the characters appropriate to *it* in accordance with its environment. There are no such things as "hereditary" characters. All these modes of expression date back to a pre-scientific stage in the history of genetics, and these fruitless discussions will continue until they are abandoned (cf. Part II, p. 442).

What people really have in mind when they discuss the relative "importance" of "heredity and environment" is usually the question of whether the G -type of cells is liable to change with a changing environment. Most of our experience leads us to think of it as being remarkably constant, and we begin by conceiving it in this way. But if we adopt the doctrine of evolution we are compelled to modify this belief. Moreover, there are the recent experiments which seem to require the assumption of such changes. The whole question is extremely obscure and

our ignorance in this region is profound. The problem which most exercises Neo-Lamarckians is the question: How is "adaptation" involving change of G-type in correlation with changing conditions of life or habit possible? Neo-Lamarckians are people who believe that it is not only possible, but that there is experimental evidence that it actually happens. Others deny that the experiments require such an interpretation, and some deny that it is possible. But such a question cannot be discussed without first undertaking a thorough analysis of all the difficult problems raised by the notion of adaptation and the consequences of the doctrine of evolution. We might find, after such an investigation, carried out independently of the analysis of genetical and embryological ideas, that we were led to make different assumptions from those suggested by the latter, and this might indicate ways in which adjustments could be made to enable the requirements of both lines of approach to be satisfied. But until this has been done in a much more thorough manner than has yet been contemplated it seems premature to hope for such a comprehensive synthesis.

It will have been noted that I have tried to state all the important propositions in terms of the relations of difference and non-difference. This keeps close to the actual procedure of thought in an experimental investigation, and enables us to avoid having to make "absolute" or "metaphysical" assertions about the entities involved. It has been said that "genes only exist in the minds of geneticists." But if this were so genetics would be a branch of psychology, and this does not seem to be the case. If it is so then genes are clearly not the things that geneticists are talking about. A "gene" is simply *that which is different* in two cells which "belong to different

G-types" or "are genetically different." If you go on to add that *that which is different* in such cases in an "entelechy," or an "unconscious memory" or a "supply of chemicals," then such further assertions are significant only if they lead to the discovery and systematization of further knowledge relating to data of the same sort as those which led to the assumption of the genetic difference in the first place, i.e. something perceived. They do not take us any nearer to a hypothetical realm "behind the scenes" where the "secrets of nature" are revealed.

My chief aim in these articles, apart from the attempt to clear up *particular* muddles in relation to these topics, has been to illustrate and urge the *general* desirability of devoting some little attention to the linguistic and logical aspects of biology. If we are willing to take endless trouble, and exercise unlimited patience, in order to attain precision in experiment, it seems strange that we should grudge the effort needed for a precise analysis of our logical procedure, and for the accurate expression of our results. What seems to be a common point of view has recently been expressed as follows:

The nature of the research worker is such that once a scientific puzzle clears itself up he loses real interest in it. He grudges even the time for writing up his results in full and is impatient only to get to grips with the further problem.

Within its limitations this is doubtless a highly meritorious attitude, but it clearly needs supplementation (if the scientific world is not to be peopled entirely by hermits and solipsists) by those who do not grudge the time requisite for the clear intercommunication and interpretation of results. If there is too little time to write up results "in full," there is surely no time at all for the writing of misleading

popular books, or for quarrels which are largely the outcome of the neglect of just those precautions which are an essential pre-requisite of any exact theoretical biology.

Our language, if it is to be adequate to deal with a given realm of fact, must have a logical structure of the same degree of multiplicity as that of the realm of fact itself. It is therefore useless to complain in one breath that biology is backward because organisms are so complicated, and then to refuse in the next to entertain complex ideas, or to construct a language which is capable of giving expression to them. A discussion of embryological topics and their relation to genetics with

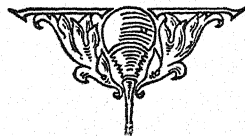
our current conceptual and linguistic apparatus is like performing a modern surgical operation with a pair of nail scissors and a potato peeler.

I hope the foregoing analysis will make some amends for the very muddled discussion of the same topics in the first part of Chapter IX in my book *Biological Principles*, which was muddled because I had not then freed myself sufficiently from the difficulties inherent in our current notions and language.

It is fatally easy to make mistakes in these matters. If, therefore, any reader is able to detect flaws in the above reasoning I shall be very grateful to have them pointed out.

LIST OF LITERATURE

- | | |
|---|--|
| (1) DE BEER, G. R. Embryology and Evolution. 1930. | (7) MORGAN, T. H. Critique of the Theory of Evolution. 1919, p. 144. |
| (2) DÜRKEN, B. Experimentalzoologie, 2te Aufl. 1928, p. 565. | (8) WEISMANN, A. The Germ Plasm. (Eng. trans.) 1893, p. 134. |
| (3) GURWITSCH, A. Versuch einer synthetischen Biologie. 1923. | (9) WOODGER, J. H. The "concept of organism" and the relation between embryology and genetics. Part I. QUART. REV. BIOL., Vol. V, p. 1-22. |
| (4) JENNINGS, H. S. Prometheus. 1925. | (10) ———. The "concept of organism" and the relation between embryology and genetics. Part II. QUART. REV. BIOL., Vol. V, pp. 438-463. |
| (5) JOHNSON, W. E. Logic, Part I, 1921, p. 173. Part III, 1924, p. 84. | |
| (6) MAXIMOW, A. In Special Cytology, ed. E. V. Cowdry, Vol. 1, pp. 347-8. | |





THE PRESENT STATUS OF THE PROBLEMS OF ORIENTATION AND HOMING BY BIRDS

By LUCIEN H. WARNER

White Plains, N. Y.

THE phenomena of migration and homing are quite distinct and much confusion has arisen from the fact that they have frequently been treated together in theoretical discussions. It should be noted that in the first migration of a bird's life it flies from the region of its birth to a region to which it has never been before. This alone distinguishes it from homing. The latter phenomenon, though it may involve flight *from* a point never before visited, always involves flight *to* a known point. The goal is a nest or cote where the animal has succeeded in establishing itself. There are other differences. Migration is a distinctly seasonal affair. Homing, in certain species, can be demonstrated at any time of the year. In fact it may be conjectured that *all* species will attempt to home at any time of the year during which they possess an established home to which to fly. Species vary widely, however, with respect to the distance over which they can successfully home.

There are two questions which must be answered regarding both migration and homing. These are: (1) What is it that impels the bird to home, or to migrate? (2) How does the bird succeed in finding its way in the homing or migratory flight? Unfortunately, only the first has received emphasis in discussions of migration, and only the second in discussions of homing. With respect to the first question, it may be conjectured that migration and homing have little in common.

With respect to the second they probably are related, for it is extremely likely that whatever means of orientation a bird possesses are utilized in both homing and migratory flight.

We shall not discuss the question of what impels birds to home. Investigators seem simply to have accepted the fact that they do home and have not volunteered explanations. But the problem of how a bird finds its way home has given rise to a number of hypotheses which must now be considered. Although homing over at least short distances could, no doubt, be demonstrated in any bird possessing at the time an established nest, it is the pigeon which has been rewarded with the most attention since this semi-domesticated bird has evidenced an unusual capacity. The facts, briefly, are these. Certain pigeons, but especially the older and previously trained individuals, succeed in returning to their cote when transported to and released from a distant point even though they may not have previously visited the release point. The usual classification of the hypotheses advanced to cover this behavior is based upon the stimulus which is assumed to orient the bird. Our discussion will make use of the following headings:

- I. The assumption that stimulation emanating from the cote itself directly affects the bird.
- II. The assumption that the bird is sensitive to slight magnetic variation.
- III. The assumption that retention of the

effects of stimulation received during the outward journey results either in exact retracing of that journey or in an immediate orientation toward the côte.

- IV. The assumption that, upon release, the bird flies without orientation until it encounters stimuli (usually visual) which it had encountered on previous flights, and that these stimuli release those responses which had formerly been successful.

HYPOTHESIS I

Hachet-Souplet (12) is one of those who venture the suggestion that birds orient as a result of direct stimulation by the goal. He calls attention to the extremely acute eyesight of birds and suggests that this stimulation is visual. He supposes that a bird flies to great heights in order to get this direct view, but that such heights need not be as great as would be supposed because of the refraction of light. The view from tremendous distances, even though dim and vague, will arouse in the bird the feeling, "*déjà vu*." He cites instances of homing birds which, upon being released, have flown upwards in spirals until they disappeared from view. This hypothesis is perhaps adequate for all shorter flights. No doubt a bird will respond to direct visual stimulation by the goal when such is available. That homing over distances of several hundred miles can be accounted for on this basis alone is quite unlikely. On data supplied by Johnson on the visual acuity of the chick (14) Watson and Lashley (38) have calculated the size of an object which could be distinguished at various distances. At a distance of 582 miles, for example, there would be comprised in a visual angle of 4' (the limit of acuity in the chick) a distance of 6.8 miles. There is no reason to suppose, however,

that the chick's visual acuity can fairly be taken to represent that of birds capable of extended flight. Watson and Lashley present further calculations indicating the altitude to which a bird would need to fly in order to be directly stimulated by light reflected from the goal. At distances of a hundred miles or more the necessary altitude is beyond that to which birds customarily fly. Duchâtel (in a letter quoted by Hachet-Souplet (9)) avoids the latter difficulty by assuming that birds are responsive to infra-red rays and by further assuming that these rays follow the curvature of the earth. Unfortunately, neither assumption is true (36).

The recently proposed theory of Casamajor (1) should be mentioned under this heading since it may involve the supposition that from the region of the côte there may emanate characteristic magnetic influences which the bird can distinguish from other such influences. Casamajor's suggestion will be considered in the next section.

HYPOTHESIS II

The chief reason for advancing the assumption that birds are sensitive to electro-magnetic stimulation is to be found in the difficulty of explaining their behavior in terms of their known senses. Thauziès (29) and others cite cases wherein delay in the return of homing pigeons coincided with the occurrence of electrical storms. Such data as exist are entirely inadequate. Besides, such storms might affect the bird through other modalities, since they are accompanied by changes in atmospheric pressure, general visibility, and so on. Maurain (17) has called attention to the fact that organisms, generally, are insensitive to far more intense stimuli of this sort than those which are assumed to guide the bird.

Were birds dependent upon such stimuli in their orientation they would become most confused when flying in the neighborhood of electric cables. There has been no indication of such confusion. In a recent article, however, Michel (19) describes behavior in pigeons which is interpreted as demonstrating sensitivity to electro-magnetic influences. When the pigeons in the course of a homeward flight approached a radio station which was at the time sending messages they became confused, ceased their direct homeward flight and flew about at random. Only when they happened to fly beyond the immediate neighborhood of the station did they resume the homeward flight. Such bewilderment was not observed when the radio station was not operating. These observations suggest that a systematic study of the matter should be made.

An argument frequently used against the contention that birds are sensitive to magnetic disturbances is that there is no known organ which might be considered the receptor. The semi-circular canals have been suggested but experimental evidence that they are affected by such disturbances is wanting.

Even supposing birds to be capable of responding to slight variations in the earth's magnetism, it is difficult to understand how they could make use of this capacity when released at an unknown point. A compass would be of no use without a chart. Viguier (33) has assumed that a bird possesses such acuity that it is capable of detecting the angle of "dip," i.e., the deflection from the horizontal of the magnetic force. Since this varies only from 90 degrees at the magnetic pole to 0 degrees at the magnetic equator, it should be noted that a bird would have to discriminate differences in deflection of well under one degree in order to estimate its latitude within a hundred miles. It

is not clear how its longitudinal position could be ascertained. Casamajor (1) claims a far less specific and accurate sensitivity to terrestrial magnetism. He suggests that when a bird lives for a time in one place it becomes accustomed to certain sensory cues characteristic of that place alone. When released at a distance from home it flies in one direction and then another but constantly selects the direction which results in cues most resembling those of the home region. While recognizing that there are many factors operating, he believes terrestrial magnetism to be the most important. In support of this belief he presents the results of his own observations and those of others which indicate the unimportance of cues of other modalities. Finally he reports instances in which pigeons equipped with magnetized headgear have failed to home while similar birds equipped with non-magnetized headgear have been successful. Verdict on Casamajor's suggestion must await further data.

HYPOTHESIS III

Reynaud (23) (24) (25) has suggested the retracement theory. The bird is supposed to register in some way all the directions followed on the outward journey, even when it is passively transported. These impressions (chiefly of semi-circular origin) are in some way stored up and when the bird is freed they are released in the reverse direction, guiding it home over the same course. In favor of this theory are presented instances of birds brought to the release point by a circuitous route which required more time to home than those brought to the same point directly. It has not been difficult for other writers to collect as much similar evidence against the theory. Birds which have died on the homeward journey have occasionally been found along the route

over which they had been taken on the outward journey. On the other hand, such birds have been found at many other points including those directly opposite the direction of the cote. Bonnier (as quoted by Watson and Lashley (38)), being persuaded that sometimes pigeons homed so promptly that they could not have retraced, adopts a supplementary theory to account for such instances. He assumes that throughout all the twistings and turnings of the outward journey the bird holds fast to the memory of the *direction* of its cote. If it has succeeded in making exact allowance for all such change in direction, it will, at the moment of release, be able to fly at once in the correct direction.

These theories are susceptible to experimental test for, if the bird is dependent upon sensory cues received during the outward journey, elimination of these cues should render homing impossible. Exner (8) reports successful returns by birds treated during the outward journey in the following ways: anaesthesia; rotation; electrical stimulation.

HYPOTHESIS IV

Schneider (28) claims that homing pigeons do not possess an inborn "sense of direction" or any mysterious sensory capacity, but that they gradually acquire a knowledge of the topography of, first the immediate environment of their cote, and then a greater and greater portion of the surrounding country. He believes that this topographical memory applies principally to prominent visual cues such as large optical patterns formed by hills and valleys and villages. A bird released in unknown territory is at a loss until it happens upon some familiar visual pattern whereupon it orients itself accordingly and flies homeward.

The evidence for this theory is extensive but can be summarized under three headings.

1. *Homing ability is vastly improved by training.* Pigeon fanciers find that only after a long training period are their birds able to home successfully over long distances. Young birds or birds raised in confinement are poor homers. Such training must strengthen the bird's tendency to seek its home and must increase its flying ability. But it probably also familiarizes the bird with the territory over which it is trained. That this is an important factor in determining further homing is indicated by the fact that training in a given direction does not result in as successful flights from points in the opposite direction. Riviere (26) emphasizes the painstaking care with which racing pigeons are trained. They are treated at first "like fools" but the farther the training takes them and the more experience they have, the bigger jumps of unknown country they may safely be tested upon. He also stresses the fact that racing pigeons are trained and raced entirely in one direction from the point of release to the home cote.

2. *There is great variability in the time of returns.* When a large number of pigeons from the same cote are released a few minutes apart it would be expected that they would return at approximately the same time were they all being guided by a cue operative at the moment of release (as assumed in other theories). Any variation would be due to individual differences in flying speed. As a matter of fact the first bird home may arrive twelve hours after the release while the others may come straggling in one, two, three days, or a week later. This great variation in the time of return is what would be expected if it is true that the

birds fly about (singly, since released singly) until they happen onto familiar cues.

3. *Increase in the length of distance to be covered increases the average elapsed time out of all proportion.* Were homing determined by cues effective from the moment of release we would expect that doubling the distance to be flown would little more than double the time required. It more nearly quadruples the time required, on the average. Again, this is what would be expected according to this theory, since the amount of territory to be covered by a bird before it might chance upon a familiar object would be increased in more nearly a geometric than an arithmetic ratio with increase in distance from the côte. Hodge (13), especially, has emphasized the point that the time taken for the return is usually far in excess of that which would be required by the bird to fly in a straight line, even at a leisurely pace, from the point of release to the côte. He furnishes estimates indicating that the elapsed time is usually more than sufficient to permit the bird to fly in ever widening spirals until it must of necessity fly over a point familiar to it. Were birds capable of direct flight home over unfamiliar territory it would be expected that they would utilize this ability to reach food and protection by more frequent rapid returns.

Of the experiments in support of the hypothesis that the released bird wanders pretty much at random until it happens upon known landmarks, there is one which deserves specific mention. Rabaud (21) reports that a group of pigeon fanciers released at sea 5000 pigeons at distances of 146,200,300 and 500 kilometers west of Croisic. The results show that the speed of the return flight decreases with an increase in distance far more than could be accounted for by fatigue.

For the 200 kilometer group it was 75-99 kilometers per hour, for the 300 group it was 60 and for the 500 group, 40. Likewise the percentage of returns diminished sharply with increase in distance. Of the 1500 released at 500 kilometers but 300 returned in two days. The remainder were found scattered in all directions (England, Spain, Portugal, Algeria, Cape Verde, Egypt, The Caucasus). "In short," concludes Rabaud, "return to the point of departure became a matter of chance."

Lest the impression be given that the theory under consideration is in all cases adequate, the work of Watson and Lashley (38) on homing of untrained birds will be reported at this point. These experiments are among the very few on homing that are above severe criticism. The subjects, noddy and sooty terns, were captured during their brief breeding season on Tortugas Island (on the Gulf of Mexico, 65 miles west of Key West). These were marked and transported by boat to the points of release by one observer while the other kept watch of the birds' nests and noted the returns. If the returns were made in a straight line they would in every case be over water the whole distance. From most of the release points the birds might have flown within sight of land practically the entire distance, although this course would have been somewhat longer. In no case was the flying time so short as to rule out this possibility. In general it is to be noted that with increase in distance there is decrease in the percentage of returns. The data on speed of return are not entirely reliable as the writers point out that several hours or days might sometimes have passed between the return of a bird and its observation. In the following summary of these flights the data on the two species of terns have been combined since there were not significant differences.

Certain flights (New York, Mobile) have been omitted since the lack of returns were apparently due to the poor condition of the birds upon release and to shortage of food supply. The longest flight (855 miles) was from Galveston, Texas.

Distance in statute miles	No. birds released	No. returns	Time
19½	2	2	2½ hours
44½	2	2	1½ hours
65½	26	24	13 h. to 11 d.
108	4	4	1 d. to 1½ d.
418	2	0	
461	7	2	3 d.
585	10	8	3 d. 22½ h. to 7 d. 21 h.
720	2	2	11 d. 13 h. & 17 d. 2 h.
855	10	3	6 d. 2 h. to 11 d. 23½ h.

Although it is true that these birds were "untrained," there is no evidence that they were entirely unacquainted with the regions of the flights. It might be argued that those few birds which succeeded in homing over the longer distances had flown without specific orientation until they had chanced upon a stretch of the shoreline with which they were acquainted. The elapsed time in every case was ample for a vast amount of random exploration. The data presented are insufficient to disprove this possibility. Nevertheless, they suggest the operation of some means of orientation at present unknown.

While the learning theory (Hypothesis IV) might refer to stimulation from any modality, it is the visual which has been particularly emphasized. Many writers have noted that homing is most prompt on days of good visibility, that fog and night delay returns. Blind birds appear incapable of homing even over short distances. After a snow-fall it has been reported that returns are considerably delayed, presumably on the basis of the changed appearance of the country side and the disguising of landmarks. Obser-

vational and experimental investigation has indicated that, as compared with other animals, the sense most highly developed in birds is vision. It would seem reasonable to suppose, therefore, that it would be an important factor in homing. On the other hand it is obvious that this would not exclude the use of other available cues.

In addition to the four main conjectures discussed above, it is also possible that there exist certain air conditions sufficiently constant to serve as cues by which flight may be directed. Cathelin (3) suggests that further study of the equinoctial air currents, which he calls "The Gulf Stream of the aerial sea," may reveal conditions which would serve as adequate guides. However, this theory seems to be more applicable to the problem of migration than to that of homing.

Cyon's hypothetical Spürsinn (5), an assumed acute sensitivity to temperature and wind direction having its seat in the nasal region, seems to be definitely disproven by experiments of Watson and Lashley (38) and need not occupy us further.

In summarizing it should be emphasized that no one of the four hypotheses advanced or even a combination of these can be accepted as an adequate description of all homing behavior. Direct stimulation by the cöte itself (Hypothesis I) and the maintenance of an orientation toward the cöte during the outward journey (Hypothesis III) may apply to very short homing flights but can hardly apply to those over long distances. There is as yet far more evidence against than for sensitivity of birds to terrestrial magnetism (Hypothesis II). The learning theory (Hypothesis IV) appears to be more generally applicable to homing behavior than do any others.

LIST OF LITERATURE

- (1) CASAMAJOR, J. 1927. Le mystérieux "sens de l'espace." *Rev. sci. Paris*, 65: 554-65.
- (2) CATHÉLIN, F. 1919. Comment l'oiseau retrouve-t-il et aborde-t-il son nid? *Rev. franc. Orn.*, 6: 110-4.
- (3) —. 1920. Les migrations des oiseaux. Paris, Delagrave, 165 p.
- (4) CLAPARÈDE, E. 1903. La faculté d'orientation lointaine (Sens de direction—sens de rotation.) *Arch. Psychol. Genève*, 2: 133-80.
- (5) CYON, E. VON. 1900. Raumsinn und Orientierung. *Pflügers Arch.*, 79: 211-302.
- (6) —. 1900. L'orientation chez le pigeon voyageur. *Rev. sci. Paris*, 37: (1st semester) 353-8.
- (7) DUSOLIER, M. P. 1903. Ce que peut faire le pigeon voyageur. *Rev. sci. Paris*, 40: (2nd semester) 691-2.
- (8) EXNER, S. 1893. Negative Versuchsergebnisse über das Orientierungsvermögen der Brieftauben. *Sitz Ber. Akad. Wiss. Wien. math.-naturw. Kl., Abt. III*, 102: 318-31.
- (9) HACHET-SOUPLET, P. 1901. De la faculté de direction à grandes distances chez le pigeon voyageur et chez les animaux en général. *Ann. Psychol. zool.*, 1: 22-6.
- (10) —. 1902. Le problème psychologique du pigeon voyageur. *Ann. Psychol. zool.*, 2: 33-51.
- (11) —. 1902. À propos du pigeon voyageur. *Ann. Psychol. zool.*, 2: 51-60.
- (12) —. 1909. Quelques expériences nouvelles sur les pigeons voyageurs. 6th. Int. Cong. Psychol., 663-7.
- (13) HODGE, C. F. 1893. The method of homing pigeons. *Pop. Sci. Mon.*, 44: 758-75.
- (14) JOHNSON, H. M. 1914. Visual pattern-discrimination in the vertebrates. II. Comparative visual acuity in the dog, the monkey and the chick. *J. Anim. Behav.*, 4: 340-61.
- (15) LASHLEY, K. S. 1915. Notes on the nesting activities of noddly and sooty. *Carn. Instn. Pub.* 211: 61-83.
- (16) LEE, A. R. 1923. Homing pigeons' care and training. *U. S. D. A. Farmer's Bull.* 1373: 15 p.
- (17) MAURAIN, C. 1923. Les propriétés magnétiques et électriques terrestres et la faculté d'orientation du pigeon voyageur. *Nature*, Paris, 51: (1st semester) 233-8.
- (18) —. 1926. Les propriétés magnétiques et électriques terrestres et la faculté d'orientation du pigeon voyageur. *Nature*, Paris, 54: (2nd semester) 44-5.
- (19) MICHEL, Z. 1928. Les ondes cosmiques et la vie. *Rev. gén. Sci. pur. appl.*, 39: 48-52.
- (20) PAILLERETS, BONNET DE. 1927. Expériences sur les facteurs de l'orientation chez les oiseaux. *Rev. franc. Orn.*, 19: 218-64.
- (21) RABAUD, E. 1926. L'orientation lointaine et la reconnaissance des lieux. *J. Psychol.* Paris, 23: 789-825 and 885-934.
- (22) —. 1928. How Animals Find Their Way About. A Study of Distant Orientation and Place Recognition. London, Kegan Paul, Trench, Trubner, 142 p.
- (23) REYNAUD, G. 1900. The orientation of birds. *Bird Lore*, 2: 101-8 and 141-7.
- (24) —. 1902. Note sur l'orientation des oiseaux et de colombier mobile. *Bull. Inst. gén. psychol.*, 2: 218-21.
- (25) —. 1903. L'orientation des pigeons voyageurs. *Bull. Inst. gén. psychol.*, 3: 33-42.
- (26) RIVIERE, B. B. 1923. Homing pigeons and pigeon-racing. *Brit. Birds*, 17: 118-38.
- (27) ROCHON-DUVIGNEAUD, A. 1926. Enquête sur l'orientation du pigeon voyageur et son mécanisme. *Nature*, Paris, 51: 232-3.
- (28) SCHNEIDER, G. H. 1905. Die Orientierung der Brieftauben. *Z. Psychol. Physiol. Sinnesorg.*, 40: 252-79.
- (29) THAUZIÈS, A. 1898. L'orientation. *Rev. sci. Paris*, 61: 392-7.
- (30) —. 1909. Expérience d'orientation lointaine. *Arch. Psychol. Genève*, 9: 66 (only).
- (31) —. 1910. L'orientation lointaine. 6me. Int. Cong. Psychol. Genève, 1909: 263-80.
- (32) —. 1913. L'orientation lointaine des pigeons voyageurs. *Rev. sci. Paris*, 51: 805-8.
- (33) VIGUIER, C. 1882. Le sens de l'orientation et ses organes chez les animaux et chez l'homme. *Rev. phil. France étrang.*, 14: 1-36.
- (34) WATSON, J. B. 1908. The behavior of noddly and sooty terns. *Carn. Instn. Pub.* 103: 187-255.
- (35) —. 1910. Further data on the homing sense in noddly and sooty terns. *Science*, ns, 32: 470-3.
- (36) —. 1915. Studies on the spectral sensitivity of birds. *Carn. Instn. Pub.* 211: 85-104.
- (37) —. 1915. Recent experiments with homing birds. *Harp. Mag.*, 131: 457-64.
- (38) WATSON, J. B., AND LASHLEY, K. S. 1915. An historical and experimental study of homing. *Carn. Instn. Pub.* 211: 7-60.
- (39) WHITMAN, C. O. 1919. The behavior of pigeons. (Vol. 3: Posthumous Works. Editor, Harvey Carr.) *Carn. Instn. Pub.* 257: 161 p.



MITOGENETIC RAYS

By ALEXANDER HOLLAENDER AND EUGENE SCHOEFFEL

Laboratory of Colloid Chemistry, University of Wisconsin

THE problem of light emission in vital processes and in chemical reactions has often been discussed, but because of contradictory experimental results and a tendency toward an over-speculative interpretation of them much of the published work on the subject has been received with skepticism and for the most part soon forgotten.

In recent years, however, new interest has been aroused in the problem by the discovery of biological radiation and its influence on cell division. The pioneer in this work was Alexander Gurwitsch of the Histological Institute of the First Soviet University in Moscow. Since the first publication in 1923 more than forty papers on this subject have come from the pen of Gurwitsch and his co-workers. Of these, two deserve special mention. One, entitled "Das Problem der Zellteilung physiologisch betrachtet" (1) summarizes the work in this field up to 1926. A later survey article in *Protoplasma* (2) reviews the subject up to the year 1928. Inasmuch as no adequate summary of the researches carried on in this interesting field has been published in English it has seemed to the present authors worth while and desirable to prepare such a review.

Gurwitsch defines the mitogenetic effect as the action at a distance of one object upon another living object, producing an increase in the intensity of cell division in the second object. The former agent is designated the *Sender*, the latter is called the *Detector*.

The number of investigators working

on this problem is steadily increasing. The experiments of Gurwitsch were first repeated by J. and M. Magrou, later by Reiter and Gabor, and also by Siebert and others. These investigators have verified the findings of Gurwitsch, in essence at least. Others, however, Rossman for instance, obtained negative results. These experiments will be discussed in some detail.

GURWITSCH'S EXPERIMENTAL TECHNIQUE

The original experiment of Gurwitsch will serve to illustrate what is meant by the mitogenetic effect. Bulbs of the common onion (*Allium cepa*) were allowed to stand in water for some time. After the roots had grown to a length of twelve to thirteen centimeters they were examined and the one that was most perfectly formed and had the most symmetrical tip was chosen for experimentation, and the rest cut away. A close fitting glass tube was then slipped over the single remaining root, which was supported in a horizontal position and kept moist during the experiment. This root served as the sender. A second root, to serve as detector, was prepared in the same way and placed in a glass tube; this time, however, the root extended beyond the length of the glass tube for a distance of about five millimeters. Over the protruding end of this root another glass tube was placed, leaving, however, about two millimeters of the root exposed. This preparation was, of course, also kept moist.

The two roots were next brought close

together, the detector in a vertical position, the sender in the horizontal position with the axis of the sender pointing directly at the exposed section of the detector root. This adjustment was very carefully made by means of a telescope so that "the projected axis of the sender root struck the detector exactly in the median line." The whole set up was held firmly in position by a rigidly built

the number of mitotic figures to the right and left of the median line counted. The experiment revealed "a regular sharply circumscribed preponderance of mitoses in the center of the induced side of the root." The excess of mitotic cells on the side toward the sender over those on the opposite side was about fifty per cent. The results of a determination are given in Table I.

TABLE I

Induced side.	29	36	58	55	62	56	50	62	36	33	39	37
Not induced side.	33	31	40	36	35	42	42	36	40	35	39	41
Difference.	-4	5	18	19	27	14	8	26	-4	-2	0	-4

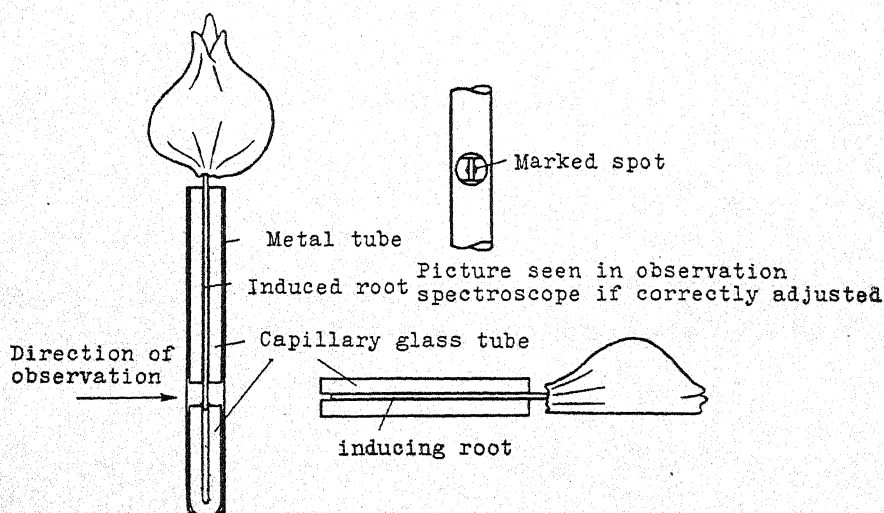


FIG. 1. EXPERIMENTAL ARRANGEMENT FOR GURWITSCH'S FUNDAMENTAL EXPERIMENT (INDUCTION OF ONION ROOT BY ONION ROOT THROUGH AIR)
(From Reiter und Gabor, Zellt. und Str.)

frame. It was most important that the adjustments should be carried out with extreme care since on them the success of the experiment rested. After remaining in this position from two to three hours the sender root was removed, the detector allowed to stand a certain length of time, then the direction of induction was marked and the root was prepared for sectioning. The last five millimeters of the root were cut in longitudinal sections, parallel with the direction of induction, and

The outcome was not materially different when a thin crystalline quartz plate was interposed between sender and detector. Gurwitsch (3) considered that these experiments proved the existence of a radiation, which he called mitogenetic rays.

YEAST AS A DETECTOR

Baron, a collaborator of Gurwitsch, found that yeast could also be used as a detector. He determined the increase in

the number of buds under definite conditions with and without the presence of the sender, and ascertained that, while the number of buds increased by 15 per cent without a sender, the increase was of the order of 25 per cent with a sender. Since in comparison with the onion, yeast is more easily handled, it is now generally used as a detector in place of onion root, which might now be said to have only an historical interest. The technique of this method is described by Gurwitsch (4) in Abderhalden's *Handbuch der biologischen Arbeitsmethoden*. In the same publication are to be found descriptions of the use of other detector materials, such as the corneal epithelium of frogs, Amphibia, etc.

using onion sole, muscle tissue, and cancer tissue as senders.

WHAT TISSUES EMIT RAYS?

Not only onion roots, but many other plant tissues and parts can be used as senders. Indeed Gurwitsch seems to be justified in speaking about the universal character of mitogenetic radiation. As an illustration, the following list of materials is presented, taken from the review article by Gurwitsch in *Protoplasma*: (1) Bacteria. The induction effect was first shown in these organisms by J. and M. Magrou with *Bacterium tumefaciens*, and later described by Baron, from Gurwitsch's laboratory, for different

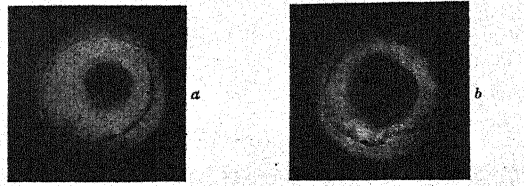


FIG. 2. MAKRO EFFECT WITH YEAST AFTER THREE DAY EXPOSURE
a = control; b = induced drop. (From M. Baron, *Abd. H. d. biol. Arb.*)

According to Baron it is possible to produce the mitogenetic effect in a manner recognizable to the naked eye. He used a standard hanging drop containing about 8000 "old" yeast cells per cubic mm. in a moist chamber, which he closed with a thin quartz plate. Under this plate he placed a container with young rapidly growing yeast. A control chamber was prepared in identically the same manner, except that the quartz plate was replaced by a glass plate. The "macroeffect" shown in the accompanying figure became evident after three days.

The yeast technique has been tried with apparent success by the authors of the present article. Experiments were made

kinds of bacteria. (2) Yeast. The methods employing these organisms were first described by M. Baron, and later verified and used by Siebert. (3) Cleavage stages of animal eggs, in particular the animal pole of amphibian embryos in the morula stage (A. Anikin), and sea urchin eggs prior to cleavage (Frank and Salkind) as well as during the second and third cleavage stages (Salkind). (4) The yolk of the hen's egg during the first two days of incubation. Only the yolk from the subgerminal area was used, and this was found to lose its power to radiate after the beginning of the circulation. (5) Various portions of plant seedlings, especially of *Helianthus* (Frank and Salkind),

in particular the root tips (Rawin), the cotyledons, and plumule. (6) Leptom bundles of potato (Kisliak and Statkevitch). (7) Fresh onion sole brei [The word "brei" means a pulp prepared by the grinding of tissue material.] (A. and L. Gurwitsch, Reiter and Gabor.) (8) Day old sterile beet brei (Anna Gurwitsch). (9) A brei made from young tadpole heads (A. Anikin, Reiter and Gabor). (10) Blood of frogs and rats (Gurwitsch, Sorin). (11) Corneal epithelium of starved rats (L. Gurwitsch). (12) Contracting muscle (Siebert, Frank). (13) Neoplasms (Gurwitsch, Siebert, Reiter and Gabor).

According to Gurwitsch it may be said in general that meristematic tissues do not give off rays, but that their mitogenetic impulse comes from other sources which themselves do not usually show cell division. Malignant cancerous tissue seems to form the only exception known to this rule; it is rich both in mitotic cells and in mitogenetic rays. Sea urchin eggs have the ability to radiate and to form mitotic figures, but in this case division and radiation have been shown to alternate. Gurwitsch mentions repeatedly that intense cell division and ability to radiate are not connected with each other.

THE WAVE LENGTHS OF MITOGENETIC RAYS

Any proof of the existence of the rays from a physical standpoint demands a study of their properties. As is evident from the experiments already described, a thin plate of crystalline quartz does not materially weaken their effect. But if this quartz plate is covered with a thin layer of gelatine the rays cannot penetrate. This definitely indicates that the rays must be short in wave length. They appear to show all the properties of light in the ultra-violet region. The rays can be reflected and they move in straight

lines, as the accompanying figures indicate. Artificial sources (iron arcs, aluminium sparks, and the like) can also be used as senders. Frank, a coworker of Gurwitsch, has used an arc between aluminium electrodes as sender, before a large quartz spectrograph. In place of the photographic plate he used small blocks of agar covered with a fine layer of yeast cells. Each block covered a certain part of the spectrum, and he found that the greatest effects were evident in the wave length region of 200 to 240 $m\mu$. He found further that an electrically irritated muscle which he used as sender before a small quartz spectrograph gave a distinctly greater increase of buds in the detector yeast culture between the wave lengths of 199 and 237 $m\mu$ than was observed at other wave lengths.

THE WORK OF REITER AND GABOR

The most important work on the subject of mitogenetic rays, aside from that of Gurwitsch and his students, is that of Reiter and Gábor (5). The authors last mentioned have recently published an excellent monograph on the subject, the product of three and a half years of experimental study. In the main their work substantiates that of Gurwitsch, but their methods of sectioning and counting are different. They used cross sections in place of longitudinal ones. In figure 4 a typical cross section is given, showing the effect of the radiation. The experimental set-up was the same as that of Gurwitsch. Like the latter author Reiter and Gabor come to the conclusion that a radiation occurs, but they believe its effect is to retard mitosis with the result that more cells are to be found in the mitotic stage at any one time than would be found in this state under ordinary conditions.

Like Gurwitsch they were unable to detect any radiation from narcotized roots,

but in contrast to his results they found that brei made of onion sole [short stem of onion bulb] radiates only when exposed to visible light. They verified the discovery of Gurwitsch that a brei

were likewise found to be inactive. Malignant tumors from fresh operative material as well as experimental malignant tumors gave the mitogenetic radiation, but benign tumors were ineffective. They

TABLE II

Number of agar block.....	1	2	3	4	5	6
Spectral region in $m\mu$	186-199	199-219	220-240	240-270	280-320	320-360
Induction effect.....	-3.2%	+43%	+30%	+0.5%	+3.2%	-2%

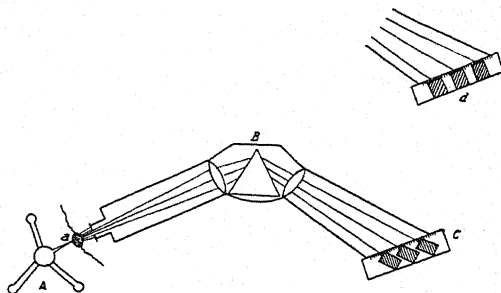


FIG. 3. SCHEMATIC VIEW OF EXPERIMENTAL ARRANGEMENT FOR SPECTRAL SEPARATION OF MITOGENETIC RADIATION OF A TETANIZED FROG-SARTORIUS

(A) Base with sartorius and connecting electrodes. (B) Schematic cross-section of spectroscope and path of rays. (C) Glass plate with marks showing the different wave lengths of spectrum; on glass plate are the agar blocks with yeast culture. They are arranged in the main figure so that radiation hits them vertically. In the side figure (D) with common front and oblique angle of radiation. (From G. Frank.)

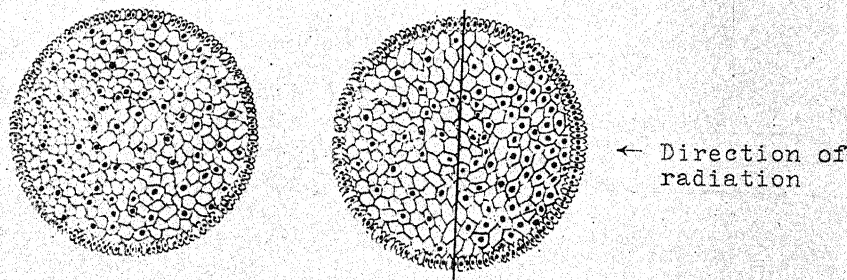


FIG. 4. SCHEME OF A NORMAL UNINFLUENCED AND OF AN INFLUENCED CROSS-SECTION OF A ROOT

The median line separates the half turned towards the sender and the one turned away. (From Reiter and Gabor.)

made of the heads of tadpoles would radiate whereas body brei was inactive. In contrast to other investigations yeast and muscle were found ineffective; however, the experimental conditions were somewhat different. Many other tissues

found further, as had Gurwitsch and his coworkers, that the radiation can be reflected and broken up by refraction and travel in straight lines. In order to show that an external chemical influence was not the cause of the effect Reiter and

Gabor enclosed an onion root, with a bit of the bulb attached, in a quartz tube, which was then sealed and exposed to the sender; this experiment was successful.

In order to determine the wave length of the emitted rays Reiter and Gabor used a brei of onion sole as sender, placed before a specially built small quartz spectrograph. As detectors onion roots

totic activity was observed also around 280 $m\mu$. Between 290 and 320 $m\mu$ an antagonistic effect could be recognized.

The reason for the discrepancy in wave lengths found by Gurwitsch and those found by Reiter and Gabor may lie partly in the experimental technique. The latter authors used a much longer time of exposure than did Gurwitsch. The ques-

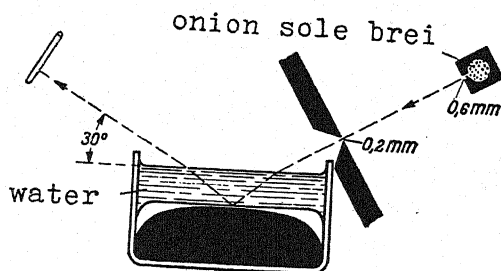


FIG. 5. REFRACTION OF MITOGENETIC RAYS IN WATER AND REFLECTION FROM MERCURY
(From Reiter und Gabor, Zellt. und Str.)

Cell division
causing influence ↑

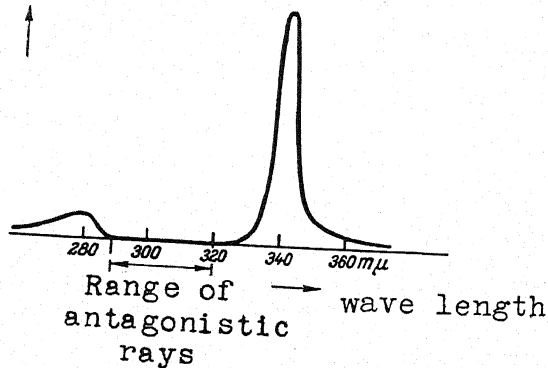


FIG. 6. DEPENDENCE OF INFLUENCE ON INDUCTION OF GROWING ZONE OF ONION-ROOT FROM THE WAVE LENGTH
(From Reiter und Gabor, Zellt. und Str.)

were used in place of photographic plates. They found that the emitted radiation fell in the neighborhood of 330 to 340 $m\mu$. In other experiments they used artificial sources for the light, placing these before a large spectrograph, and found in contrast to Frank that the wave length 340 $m\mu$ gave the most favorable results, but that a slight increase in mi-

tion, however, has by no means been cleared up as yet.

Inasmuch as the sunlight contains among others the wave-lengths around 340 $m\mu$ it might be expected to exert a favorable influence on mitotic activity, but since sunlight also contains the antagonistic wave lengths no beneficial effect is imparted. Reiter and Gabor have applied

the results of their investigations to therapeutic treatments.

THE WORK OF OTHER INVESTIGATORS

In Paris, J. and M. Magrou (6), working independently of the Gurwitsch school and experimenting on *Bacterium tumefaciens* and cancerous tissue, reported verification of Gurwitsch's results.

Siebert (7) was the first to find that working muscles gave out the rays while muscles at rest did not. He worked not only with whole muscles but with muscle brei. He tried to repeat the experiments of Warburg (8) and reported success. According to his belief the rays emanating from muscle originate in an oxidation process. In his later experiments Siebert used yeast as a detector, the effect being recognized, following the method of Baron, by a higher percentage of yeast buds in the exposed culture as against that in the unexposed control. He observed an increase also in the areas adjacent to the actual paths of the rays. He believes that, associated with the Gurwitsch mitogenetic radiation there is a so-called "*Aktionsstrahlung*."

Stempell (9), a German investigator, found that the decomposition of hydrogen peroxide could be accelerated when it was exposed to the radiation from onion brei. Furthermore he obtained a most striking proof of the effect of mitogenetic rays on the formation of Liesegang rings. This has since been discredited.

The experiments of Gurwitsch with onion root tips and yeast have also been verified in an article which has just appeared in this country (10).

PHOTOGRAPHIC METHODS

Many authors have sought to obtain proof of these rays by means of the photographic plate, but with the exception of

one very questionable case they have been unsuccessful. Gurwitsch believes that the photographic method is the least promising. Common photographic plates are not very sensitive to the radiation around 220 m μ . They might perhaps be sensitized by special treatment or Schuman plates might be used; but all these plates are less sensitive for the wave-lengths concerned than are the most sensitive plates to longer wave-lengths. It is quite possible that the rays may exist and at the same time not be detectable by a photographic plate. Researches in the laboratory of the Eastman Kodak Company have shown that several hundred absorbed light quanta are necessary to make a single grain developable. It is very possible that the number of quanta in mitogenetic rays is not sufficient to give this result. According to calculations carried out in Gurwitsch's laboratory the onion root is 600 times as sensitive as the photographic plate. It seems therefore that it will be necessary to develop a much more sensitive means of detecting rays if such very weak light phenomena are to be properly investigated. Such a detector would open up a whole new field in photochemistry. Experiments along this line are at present being carried out by Gurwitsch and his co-workers.

Of the investigations that have failed to verify the results of Gurwitsch the work of Rossmann (11) is the most outstanding. Rossmann believes that the criterion of counting mitoses is not a reliable one, and that the exact number of cell divisions in process cannot be determined with any degree of accuracy. Since Rossmann's attack Gurwitsch has published more detailed procedures, and an abundance of statistical material supporting his theory. Gurwitsch claims also that Rossmann has not repeated his experimental conditions and has also used plant roots as indicators

that were not as well suited to the purpose as is the onion root.

Gurwitsch compares the causes of the mitogenetic radiation with the causes of the radiation of fireflies, after the classical experiments of Dubois.

Another interesting bit of experimental work on onion sole brei deserves mention. If a sample of brei is kept for forty minutes or longer it ceases to give out the mitogenetic rays. Furthermore if fresh onion brei be heated to 56°C. it also ceases to radiate. However, if these two samples be stirred up together the mixture gives off radiations. In analogy with the terms used in the study of bioluminescence the two substances in the brei have been called by Gurwitsch *mitotin* and *mitotase*. These substances are assumed bodies, which have not yet been separated.

About the cause of the mitogenetic radiation of yeast and bacteria nothing is known. More is known about the radiations from animals. The results obtained from the study of blood radiation are not clear, and can hardly be adequately explained at the present stage of research.

Blood serum does not of itself give off radiations, but by the addition of oxyhaemoglobin or hydrogen peroxide it can be made to do so, which seems to indicate an oxidation reaction. While the blood of normal healthy rats gives off radiations, the blood of starved rats does not, but if a little glucose be added to the latter radiations are detectable.

If one accepts the effect as established there remain the various explanations of it which have been suggested. The solution of the difficulty which appeals to a chemist would be to postulate the existence of a reaction, probably an oxidation, which emits light during its progress. The unfortunate experience of the chemist with the radiation theory of chemical reaction would, however, teach him to be more than careful in accepting such an explanation without proof beyond reasonable doubt.

The problem is without doubt one of the most intriguing of the many scientific problems before us today. It is one in which workers both in biological and physical sciences may well be interested.

LIST OF LITERATURE

- (1) GURWITSCH, A. 1926. Das Problem der Zellteilung physiologisch betrachtet. Julius Springer, Berlin.
- (2) ——. 1929. Ueber den derzeitigen Stand des Problems der mitogenetischen Strahlung. *Protoplasma*, 6, 449.
- (3) GURWITSCH, A. UND N. 1924. Fortgesetzte Untersuchungen ueber mitogenetische Strahlung und Induktion. *Roux's Archiv*, 103-68.
- (4) GURWITSCH, A. 1929. Methodik der mitogenetischen Strahlenforschung. *Abd. Handb. d. biol. Arbeitsmeth.*, Abt. V, Part 2, Page 1401.
- (5) REITER, T., UND GÁBOR, D. 1928. Zellteilung und Strahlung. *Sonderheft d. Wiss. Veroeff. aus dem Siemens-Konzern*. Julius Springer, Berlin.
- (6) MAGROU, J. ET M. 1927. Radiations mitogénétiques et genèse des tumeurs. *Comptes Rendus, Paris*, 184-205.
- (7) SIEBERT, W. W. 1928. Ueber eine Beziehung von Muskeltaetigkeit zu Wachstumsvorgaenge. *Z. f. Klin. Med.*, 109-260.
- (8) WARBURG, O. 1914. Über die Verbrennung der Oxalsäure an Blutkohle und die Hemmung dieser Reaktion durch indifferente Narkotica. *Pflügers Arch.*, 155, 547.
- (9) STEMPPELL, WALTER. 1929. Die Lebensstrahlen. *Strahlentheraphie.*, 34-868.
- (10) BORODIN, O. N. 1930. Energy emanation during cell division. *Plant Phys.*, 5-119.
- (11) ROSSMANN, BRUNO. 1928. Untersuchungen ueber die Theorie der mitogenetischen Strahlung. *Roux's Archiv*, 113-346.



NEW BIOLOGICAL BOOKS

The aim of this department is to give the reader brief indications of the character, the content, and the value of new books in the various fields of biology. In addition there will frequently appear one longer critical review of a book of special significance. Authors and publishers of biological books should bear in mind that THE QUARTERLY REVIEW OF BIOLOGY can notice in this department only such books as come to the office of the editor. The absence of a book, therefore, from the following and subsequent lists only means that we have not received it. All material for notice in this department should be addressed to Dr. Raymond Pearl, Editor of THE QUARTERLY REVIEW OF BIOLOGY, 1901 East Madison Street, Baltimore, Maryland, U. S. A.

BRIEF NOTICES

EVOLUTION

LA VARIATION ET L'ÉVOLUTION.

Tome II. *L'Évolution.*

By Émile Guyénor.

G. Doin et Cie.

32 francs (paper)

Paris

4 $\frac{1}{4}$ x 7; viii + 414

The first part of this book, dealing with variation, has already been reviewed in these columns. With regard to evolution, Guyénor concludes that there is no good evidence of the inheritance of acquired adaptations, that mutations furnish the only basis for evolution of which there is actual evidence. However, observed mutations have always been in the details rather than in the fundamental plan of organisms. "It is impossible for us to imagine by what mechanism the different types of organization which characterise the major zoological groups can have been formed, can have been derived from one another or from ancestral forms. On this point the paleontological documents are silent." This is much like the conclusion that Clark reaches in *The New Evolution*. However, Guyénor, more cautious than Clark, does not go on to postulate that life at its very beginnings from the single cell developed simultaneously and at once in every possible direction. To us this agnostic attitude seems the wiser.

ANIMAL ECOLOGY AND EVOLUTION.

By Charles Elton. Oxford University Press

\$1.50 4 $\frac{3}{4}$ x 7 $\frac{1}{4}$; 96 New York

This little book merits the careful consideration of students of biology. The three essays, the substance of lectures delivered in the University of London on the future of animal ecology are as follows: The regulation of numbers; the significance of migrations; and the real life of animals. It is the author's opinion that

the study of the relations between wild animals and their surroundings cannot be properly conducted with a background of theory or hypothesis on the subject of evolution, that the present remarkably chaotic state of the largely unco-ordinated data that animal ecologists have collected is mainly to be attributed to the lack among biologists of an adequate philosophy of animal life, and, finally, that the time is now ripe for some such philosophy to be formulated, if only in a very tentative and preliminary form.



A STUDY OF THE PHYTOSAURS with Description of New Material from Western North America.

By Charles L. Camp.

University of California Press

\$3.50 10 x 13; x + 172 (paper) Berkeley

This report deals with a "series of 'species' of phytosaurian reptiles from a number of stratigraphic horizons in the Chinle Triassic, with comparisons between

these forms and forms previously described, and with the structure of the phytosaur skeleton." The author contributes new data on the American Mesozoic "Red Beds" and presents a "tentative classification and phylogeny of the phytosaurs, with a discussion of their relationships." Included in the work is a map showing a distribution of Chinle Triassic formation as exposed in Nevada, Arizona, Utah and Western New Mexico, also drawings, figures and plates, a literature list of 100 titles and an index.



THE PLEISTOCENE OF NORTHERN KENTUCKY. *A Regional Reconnaissance Study of the Physical Effects of Glaciation within the Commonwealth. Presented with Four Separate Geological Papers by Stephen Sargent Visser, Arle H. Sutton, James K. Roberts and Armin Kohl Lobeck.*
By Frank Leverett.

The Kentucky Geological Survey
\$1.25 $5\frac{5}{8} \times 8\frac{3}{4}$; xi + 403 Frankfort

Five papers on the geology, physiography, and climate of Kentucky.



EVOLUTION.

By E. W. MacBride.

Jonathan Cape and Harrison Smith
60 cents $4\frac{1}{2} \times 6\frac{3}{4}$; 122 New York

A brief exposition for the layman of some of Prof. MacBride's ideas concerning evolution, which are already well known to biologists.



GENETICS

THE GENETICS OF DOMESTIC RABBITS. *A Manual for Students of Mammalian Genetics and an Aid to Rabbit Breeders and Fur Farmers.*

By W. E. Castle. *Harvard University Press*
\$1.25 Cambridge

6 x 9; vi + 31 + 13 plates.

Students of genetics and rabbit breeders will be interested in this manual. It is designed to aid students of genetics to "understand better what rabbit breeders of this and previous centuries have accomplished and how they have been able to accomplish it." The rabbit breeder will better understand "the genetic constitution of his animals and so be able to alter that constitution to suit his purposes." The work includes a table showing the genetic constitution of various breeds or rabbits, a list of references and a group of plates.



PRINCIPLES OF DOG BREEDING. *A Presentation of Heredity in Dogs, the Anatomy and Functioning of the Sexual Organs, and the Selection of Bloodlines.*

By Will Judy. *Judy Publishing Co.*
\$2.00 $5\frac{5}{8} \times 8\frac{1}{2}$; 118 Chicago

There are several points to which the geneticist would object, for example the definition of mutation as "the appearance in the offspring of a quality not possessed by either parent but considered to be a quality possessed by previous ancestors. This quality newly appearing may be transmitted," and the Bruce Lowe theory of saturation, which holds that the "dam, with each successive mating by the same sire, absorbs some of the nature of the circulation of the unborn offspring until after a time she becomes saturated with the sire's blood or nature." However, these theories do not seriously mar the practical value of the book for practical breeders. There is much sound advice given which the author has gleaned from long experience in dog breeding. The book is well illustrated. There is no index.

GENETICS AND EUGENICS. *A Text-Book for Students of Biology and a Reference Book for Animal and Plant Breeders. Fourth Revised Edition.*

By W. E. Castle.

Harvard University Press

\$3.00 $5\frac{3}{4} \times 9$; x + 474 Cambridge

In this edition of one of the best text-books on genetics a fuller account is given of human heredity; the chapter on the unit characters of rodents, on which much of our knowledge of mammalian heredity depends, has also been rewritten, as well as the discussion of polyploidy, parthenogenesis, and the artificial production of mutations. Dr. Castle has the enviable faculty of presenting his subject in a clear and readable form without writing down to his readers. Perhaps that is because he really knows it himself.

PRACTICAL APPLICATIONS OF HEREDITY.

By Paul Popenoe.

The Williams and Wilkins Co.

\$1.00 $5 \times 7\frac{3}{8}$; ix + 128 Baltimore

A careful reading of this book fails to disclose the relevance of the title. Actually it is a collection of chatty essays on subjects connected with heredity, containing some amusing material, and a great deal of doubtful logic and uncritical acceptance of almost anything that fits in to make a point. A sample:

"There are a few cases where a child of superior parents is set adrift for some unusual reason. Moses is the classical example."

LA FORMATION DE L'ÊTRE. *Histoire des Idées sur la Génération.*

By Jean Rostand.

Librairie Hachette

12 francs $4\frac{3}{4} \times 7\frac{1}{2}$; 222 (paper) Paris

This excellent little book traces the history of genetics and embryology from

antiquity to the present day. There is a bibliography and an index.

LOCALIZAÇÃO DOS FACTORES NA LININA NÚCLEAR COMO BASE DE UMA NOVA THEORIA SOBRE A HEREDITARIEDADE.

By S. de Toledo Piza Junior. Piracicaba

$6\frac{3}{8} \times 9$; 98 (paper) São Paulo, Brazil

In this book the author gives his reasons for concluding that the hereditary factors are carried, not in the chromatin, but in the linin, and that they are not linearly distributed.

GENERAL BIOLOGY

INTRODUCTION À LA BIOLOGIE EXPÉRIMENTALE. *Les Êtres Organisés, Activités, Instincts, Structures. Encyclopédie Biologique VIII.*

By Paul Vignon.

Paul Lechevalier

Paris

210 francs $6\frac{1}{2} \times 9\frac{7}{8}$; 731 + 890 figs. + 24 plates (in colors) (paper)

If Plato and Aristotle in the early nineties had been awakened from their long sleep in the world-beyond, trained at the Sorbonne by Delage and Hérourard in animal morphology, especially protozoology and entomology, in drawing and painting by skilful masters, and then had devoted several years to morphological study of tropical leaf insects at Professor Bouvier's laboratory at the Muséum, they might have written this excellent book, and it would have been much to their credit. But special conditions would have been necessary: no contamination with Descartes' or Darwin's mechanistic heresies, no courses in biochemistry or biophysics. Twentieth century notions of matter, its electrons and protons, and of biological

mutations, being sufficiently idealistic, would have been permitted.

Plato would have collaborated chiefly by writing the numerous summaries and putting the book into its excellent form, with its several indices, biological and philosophical. Aristotle would have gathered material from museums far and wide, and carefully selected from the works of many modern biologists such results as lend themselves to idealism. He might perhaps have prepared the numerous fine illustrations and the colored plates of protectively-colored orthoptera.

Here we find animal behavior as viewed by Koehler, Jennings and Mast, who see things whole, rather than by such scape-grace analysts as Jacques Loeb, who is ignored, and Bohn, whose writings are listed but passed over in silence. We find a wealth of well-presented cases of psychic and infra-psychic behavior of protozoa, insects, birds and mammals; an array of beautiful forms in Radiolaria and other Protozoa are carefully described; many examples of protective resemblance are depicted with scientific accuracy and thoroughly discussed, chiefly from the standpoint of artist and poet. In brief, organisms are ideas; each has within itself, from the egg onward, its own inscrutable perfecting principle, directing its development toward utility and beauty.

Interesting examples of evolution by mutation are described in detail; natural selection no longer has a monopoly in the production of adaptations.



THE NATURE OF LIVING MATTER.

By Lancelot Hogben. Alfred A. Knopf, Inc.
\$5.00 5½ x 8½; ix + 316 New York

A series of well-written essays contributing to the current discussion of some of the philosophical problems of biology. The twelve chapters fall into three groups

dealing respectively with vitalism and mechanism; Darwinism and the atomistic interpretation of inheritance; and holism and the publicist standpoint in philosophy. The first section makes a slighter contribution in respect of either novelty or profundity than either of the other two, though it is necessary to get early into the record the author's neo-mechanistic position and its bases. Part II delivers some sound and penetrating thrusts to the up-lifters who endeavor to base their philosophy and mode of life upon biology. Hogben's main thesis is that biology has no more to do with ethical problems than does physics or algebra. As a science biology is ethically neutral. The following remarks (pp. 214-215) about eugenics have a refreshing *Klang*.

I believe that the eugenists have performed a useful task in emphasizing the need for a biological analysis of human society. The furtherance of that task will not be promoted by propaganda which overstates the achievements of the present, while underestimating the difficulties which lie ahead. Evolutionary inquiry was brought to an end in ancient Greece, when philosophy became the handmaiden of politics. Further progress was checked when philosophy became the bondservant of theology. Eugenics like Greek philosophy derived its first impulse from natural science. It soon entered into alliance with the politician. It is fast finding its most stalwart supporters among the clergy. It can only realize the aims of its founder by bringing the science of genetics into closer relationship with other methods of studying human biology and annulling the marriage of biological inquiry with political propaganda. As a private citizen the biologist is entitled to his own opinions concerning the merits of sterilizing the unfit, just as he is entitled to his own opinions on the Single tax or the advantages of capital punishment. Such opinions usually belong to his private world. In his public capacity, as a biologist, he is primarily concerned with sterilizing the instruments of research before undertaking surgical operations upon the body politic.

This book should be widely read, if for no other reason than to serve in some degree as an antidote to the sickly mys-

ticism now emitted in such great volume by eminent physicists. Unfortunately there is no index, nor a single line of bibliographic documentation. If the general reader, at whom this clever and useful book is aimed, should by any chance want to look for himself at the writings of the considerable number of persons not approved of by the author, he must do so strictly under his own steam, so far as Professor Hogben is concerned. Perhaps this is a part of the "publicist" philosophy.



THE CREED OF A BIOLOGIST. *A Biological Philosophy of Life.*

By Aldred S. Warthin. Paul B. Hoeber, Inc.
\$1.50 5 x 7½; viii + 61 New York

This essay was written in anticipation of the retirement of its distinguished author from active teaching. It is dedicated to those of his "old students who understood." The text is a development and *apologia* of the following *Credo*:

I BELIEVE IN THE LAW

In the immortality of the germ plasm and in the creative progressive evolution of life, in the variability of value of the germ plasm through heredity and environment, in the transmission of acquired characters and in the conscious improvement of the race through the laws of volative eugenics. I believe that the aim of the individual life is the protection, improvement and continuation of the immortal germ plasm, and that this is best secured by self-development in the highest possible degree through a permanent monogamic sex-partnership with limitation of offspring towards the securing of the best possible results in the progeny, and their best preparation for the continuation of the process in the next generation. In this belief the Universe is rationalized for my intelligence and reason. I accept it with optimism, relinquishing all desire for a personal immortality, and unafraid believing that whatever gods may be, the game of life will have been played squarely and according to the Law.

All biologists, not to speak of other honest folk, will not agree with all of this creed. Perhaps it is because they do not "understand."

THE NATURE OF LIFE.

By Eugenio Rignano.

Harcourt, Brace and Co.

\$2.75 5½ x 8½; x + 168 New York

In this volume of the *International Library of Psychology, Philosophy and Scientific Method* Professor Rignano further develops his solution of a problem which has vexed biologists since the days of Aristotle, the problem of the purposive aspects of living organisms, on which is based the war between mechanism and vitalism. The physico-chemical investigation of the mechanism of living processes, he finds, does not give a satisfactory explanation of their purposive character. Even if we had experimental evidence that the development of the mammary glands during pregnancy is caused by a hormone, this would in no way explain why the hormone sets in action a process which will be of use to the child about to be born rather than some useless process. On the other hand, the animistic vitalism of such writers as Driesch and Bergson is even more impotent in face of this problem. The *entelechy* and the *élan vital* are empty forms of words, explaining nothing.

With these criticisms we have much sympathy, but we are not sure that Professor Rignano's own solution really solves the problem. He wishes to postulate a new form of energy in living organisms, distinct from the forms of energy familiar in inorganic systems. It is not entirely clear to us, however, that this nervous energy is better adapted to explain the purposiveness of life than our old friends, physical and chemical energy. Perhaps we do Professor Rignano an injustice. His style, as is no doubt fitting in a philosopher, often resembles that of the Duchess in *Alice in Wonderland*. Possibly if the book were translated into a tongue understood of the people, the superiority of nervous energy to its elder brothers might

be clear. Meanwhile we sympathize with Lotka.



THE CONQUEST OF LIFE.

By Theodore Koppányi. D. Appleton and Co.

\$2.00 5 x 7 $\frac{3}{4}$; xii + 263 New York

Another popular account of what biology is all about. It attracted us but little. One or two passages will perhaps help the reader to understand our lukewarmness.

The doctrine of mimicry should be discarded. There exist neither models nor imitators, and there is no real protection by imitation.

Are we to infer that these external factors affect only one generation and cannot produce any changes in the progeny? By no means. First of all we can assume very easily that the same external factors which influence the first generation will continue to influence the second, the third, the fourth and the later generations, provided they live in the same environment. Perhaps, if the external factor influences many generations one after the other it sooner or later will affect the germ cells too. After all, such a powerful external factor as light, heat, or electricity can easily modify not only the cells of the body surface, but also the germ cells, which lie rather deep in the body. It is here that we hit upon one of the real causes of evolution, namely, that external factors produce sudden changes in the make-up of the germ cells within the animal.

As a result of his studies, Dr. Kamm is able to classify individuals as "wet" or "dry." This is what he says:

"Some individuals, the physiological wets, are extremely sensitive to the action of the Beta hormone. Others react readily to normal administration of the hormone, and they are the physiological dries.

"The fleshy type of individual is almost invariably the wet type, whereas the slender, scrawny individual is usually dry. The suggestion is therefore made that we have here possibly one of the important explanations why the former is fleshy and why the latter fails to put on weight readily in spite of an excessive taking of food and water.

"It is apparent that the portly person who is desirous of reducing must cut down on his liquid intake, as well as his intake of solid food. As for the scrawny person, gland therapy may possibly be indicated; but while the work is still in the investigative stage, conclusions cannot be drawn."

Sex life, then, when viewed from Olympian heights is perhaps the most unselfish, the most altruistic function of any being. Some insects mate, and once this life work is completed, are ready to die within a few hours.



THE HISTORY OF BIOLOGICAL THEORIES.

By Emanuel Rádl (Translated and adapted from the German by E. J. Hatfield).

Oxford University Press

\$6.00 5 $\frac{1}{2}$ x 8 $\frac{1}{2}$; xii + 408 New York

A translation of the greater part of the second volume of the original German, with unimportant revisions and omissions. The book seems to us of slight merit. As history, it rates far below Nordenskiöld's and as philosophy it makes no appeal, at least to us. The author was formerly a biologist, who worked on tropisms and on the structure of the nervous system; he has turned philosopher, and now professes natural philosophy at Prague. His career is thus reminiscent of that of Driesch (he is, like Driesch, a vitalist), but he is a much less important and less interesting worker. The book is mildly interesting.



PRINCIPLES OF ANIMAL BIOLOGY.

By Lancelot T. Hogben. Christophers

8 s. 6 d. net 5 x 7 $\frac{5}{8}$; xxiv + 332 London

A sound elementary text book, which tries to minimize technical terms, and to emphasize principles. This is, of course, what every up-to-date text-book writer says of his own work; but in the present case the effort has been rather more successful than sometimes happens.



COLLEGE BIOLOGY.

By Henry R. Barrows.

Richard R. Smith, Inc.

\$3.00 5 $\frac{1}{2}$ x 8 $\frac{1}{2}$; xv + 414 New York

Precision and clarity are great virtues

in a writer. They are, unfortunately, not always in evidence in this book.

It has been demonstrated by many breeding experiments, particularly with the fruit fly, that new characters known as mutants, not infrequently appear. Various new species have been produced in *Drosophila* which, though derived from the same ancestor, are sterile with respect to one another. This is a clear indication that in *Drosophila*, at least, new species can arise by mutation.

The figures are stated to have all been redrawn from the originals. This we regard as in many cases unfortunate.



OLD AGE. *The Major Involution. The Physiology and Pathology of the Aging Process.*

By Alfred S. Warthin. Paul B. Hoeber, Inc.
\$3.00 $5\frac{1}{4} \times 8\frac{1}{4}$; xvi + 199 New York

This is an expansion of a lecture on the pathology of the aging process delivered before the New York Academy of Medicine in 1928. It is interestingly written and well illustrated. The theory of senescence which Warthin espouses, which is not novel, is that

age, the major involution, is due primarily to the gradually weakening energy charge set in action by the moment of fertilization, and is dependent upon the potential fulfillment of function by the organism. The immortality of the germ plasma rests upon the renewal of this energy charge from generation to generation.

There is an index, but no bibliography.



CONTRIBUTIONS TO MARINE BIOLOGY. *Lectures and Symposia Given at the Hopkins Marine Station, December 20-21, 1929, at the Midwinter Meeting of the Western Society of Naturalists.*

Stanford University Press
\$7.50 Stanford University
 $6\frac{5}{8} \times 10$; viii + 277

Twenty-three papers read before the Western Society of Naturalists in December, 1929. They are grouped under the general headings oceanography, permeability, photosynthesis, early development, marine algae, and growth. The opening paper by Prof. C. A. Kofoed on the evolution of the Tintinninea is a particularly interesting and valuable contribution.



COULEURS ET PIGMENTS DES ÊTRES VIVANTS.

By Jean Verne.

Armand Colin

12 francs (cloth)

Paris

10.50 francs (paper)

$4\frac{3}{8} \times 6\frac{3}{4}$; 219

A careful study of the chemistry and physiology of animal and vegetable pigments.



HANDBUCH DER BIOLOGISCHEN ARBEITSMETHODEN. *Lieferung 329.*

Weitere Fortschritte in der Züchtung von Warmblütergewebezellen in vitro.

By Albert Fischer and Hans Laser.

Urban und Schwarzenberg

3.50 marks 7×10 ; 44 (paper) Berlin

Completes Part I of Section V with a description of the most recent advances in the technique of tissue culture.



THE BIOLOGY STUDENT.

Edited by Marguerite F. Little.

Science Publishers, Inc.

1386 W. North Ave., Baltimore

Individual subscriptions, \$2.00 for 18 issues
Ten or more to one address, \$1.00 each for 18 issues

The first number of an entertaining little nature-study magazine for school children. We wish it all success.

HUMAN BIOLOGY

THE NEGRO IN AMERICAN CIVILIZATION. *A Study of Negro Life and Race Relations in the Light of Social Research.*

By Charles S. Johnson. Henry Holt and Co.
\$4.00 $5\frac{1}{2} \times 8\frac{1}{2}$; xiv + 538 New York

In order that there might be available accurate information concerning the Negro and his status in the United States there was organized several years ago a central executive committee from sixteen national organizations which were interested in the race problem. In 1928, there was held in Washington a National Interracial Conference for the purpose of receiving the reports of the investigators and studies which had accumulated as a result of the committee's work. This book is the result of the Washington conference. Mary Van Kleeck says in the foreword that "it is neither the proceedings of the conference nor the report of an investigation. It is a synthesis of many studies put through the process of a conference which hammered it into coherence and reality." To Dr. Charles S. Johnson fell the task of gathering the material for publication.

The volume is in two parts. In the first section are discussed under twenty-five headings many of the problems of the economic and social status of the negro; his health, causes of death, hospitalization, schools, juveniledelinquency, citizenship rights, etc. Part II contains papers written for the conference. These are as follows: "The Negro in Industry", by Niles Carpenter; "The Health of the Negro", by Louis I. Dublin; "Biological Factors in Negro Mortality", by Raymond Pearl; "The Negro and the Problem of Law Observance and Administration in the Light of Social Research", by Thorsten Sellin; "The Negro Citizen", by W. E. B. Du Bois; "Race Relations", by

Herbert A. Miller. There is included in these various chapters questions which came up for discussion and summaries of the discussions.

Much labor has gone into the preparation of the volume and the records which it gives will be of service in future work. An immense amount of statistical material is presented especially in the first section of the book. There has been little attempt at this time to find remedies for many of the existing evils. Included in the work is a lengthy bibliography, a list of the organizations and committees responsible for the conference, a program of the meetings and an excellent index.



TWINS. *Heredity and Environment.*

By Nathaniel D. Mittern Hirsch.

Harvard University Press

\$2.00 $5\frac{1}{2} \times 8\frac{3}{4}$; 159 Cambridge

In this study, three groups of twins were chosen; (a) fifty-eight pairs of dissimilar twins living under similar environments; (b) thirty-eight pairs of similar twins living in similar environments and (c) twelve pairs of similar twins living in dissimilar environments. In all cases the twins were like-sexed. Statistics, which are given in tabular form in the book, were collected on anthropometric measurements, disease, history, hand writing, tests of manual and motor ability, educational and intelligence tests, etc. Among the conclusions that the author reaches are the following:

The study demonstrates that heredity and environment both contribute to the intelligence and anthropomorphic qualities of the individual, but that their contributions are far from being equal. Neither the extreme hereditist nor the extreme environmentalist is correct, but the contribution of heredity is several times as important as that of environment.

Heredity and environment vary in their relative importance in relation to specific or general traits.

Education and training vary in their influence in

proportion to the hereditary type with which they are dealing—the more intelligent the individual the more potent educational and general environmental influence.

This is an important contribution. It is written in as non-technical language as possible in order to interest the layman as well as the specialist.



GROWING UP IN NEW GUINEA. *A Comparative Study of Primitive Education.*
By Margaret Mead.

William Morrow and Co.

\$3.50 5¼ x 8; x + 372 New York

During six months of field work on the Manus Islands, Dr. Mead lived intimately with the native tribes, and acquired an excellent understanding of the development of the Manus child into an adult. She watched the baby, the child, the adolescent with a view to finding out the manner in which each one of these periods contributes towards the making of an adult. From babyhood until the near completion of adolescence, children are kings; the only demands made upon them being those of physical training. Each infant early learns to assume responsibility for its own welfare, a necessity if it is to survive a precarious mode of life, where all dwellings are flimsily "constructed over incoming and outgoing tides of the lagoon"; and adults are too busy gathering sustenance to keep watch over every movement of the child. At a remarkably early age the child has acquired great agility and nearly perfect coordination. Left to themselves the children romp all day long with no regard for discipline.

The children are allowed to give their emotions free play; they are taught to bridle neither their tongues nor their tempers. They are taught no respect for their parents; they are given no pride in their tradition. The absence of any training which fits them to accept graciously the burden of their tradition, to assume proudly the rôle of adults, is con-

spicuous. They are permitted to frolic in their ideal playground without responsibilities and without according either thanks or honour to those whose unremitting labour makes their long years of play possible.

Among these people, however, it does not happen, as some modern educational psychologists would have us believe, that the child allowed such freedom develops a richly creative spirit. The children merely play like pups, stopping only to rest so that they may play again.

In the second part of the book, the author makes pertinent comparisons between Manus and American Societies. She finds there is much similarity. The Manus peoples make their chief concern the amassing of property, enforcing morality, (quite as rigid as our most strict Puritanism) and security for the next generation.

There is . . . a curious analogy between Manus society and America. Like America, Manus has not yet turned from the primary business of making a living to the less immediate interest of the conduct of life as an art.

Marriage, maturity, and middle age are not looked forward to with any joy, for they mean only hard work to pay off debts and keep living.

Above the 35-year-olds comes a divided group—the failures still weak and dependent, and the successes who dare again to indulge in the violence of childhood, who stamp and scream at their debtors, and give way to uncontrolled hysterical rage when crossed.

This study in comparative anthropology is keen, and deserves consideration.



THE STORY OF PUNISHMENT. *A Record of Man's Inhumanity to Man.*

By Harry E. Barnes. The Stratford Co.

\$3.00 5½ x 8½; vii + 292 Boston

This book will be of interest to two classes of readers; first, sentimentalists and others who believe in the uplift; and second, bloody-minded, hard-boiled eggs

who enjoy prize fights and bull-baiting. The author gives a fair and adequate account of the various devices which have been invented for the annoyance of the convicted criminal, and a gruesome lot they are. The historical part of the book is, we think, much better than the hortatory. When Professor Barnes begins to argue as to what ought to be done to suppress crime, his logic becomes somewhat shaky, and his faith in "scientific criminology" leads him into what we can only describe as roseate optimism as to what might be accomplished. We have no quarrel with his ideals; it would be indeed a pleasanter world if Professor Barnes would reorganize the whole judicial and penal system and make it work; but we remain dubious as to whether it really would work. Also, as a taxpayer, how much would it cost? Of course, we shall be told that it would really save money, because so many criminals would be turned into valuable and productive citizens. Maybe so; but our observation is that in such reforms the taxes are paid in real money, and the savings are paid in the currency of the Musical Banks of Erewhon.



CHILDREN OF THE COVERED WAGON. *Report of the Commonwealth Fund Child Health Demonstration in Marion County, Oregon, 1925-1929.*

By Estella F. Warner and Geddes Smith.

The Commonwealth Fund Division of Publications

\$1.00 postpaid 6 x 9; 123 New York

A CHAPTER OF CHILD HEALTH.

Report of the Commonwealth Fund Child Health Demonstration in Clarke County and Athens, Georgia, 1924-1928.

The Commonwealth Fund Division of Publications

\$1.00 postpaid 6 x 9; v + 169 New York

FIVE YEARS IN FARGO. *Report of the Commonwealth Fund Child Health Demonstration in Fargo, North Dakota, 1923-27.*

The Commonwealth Fund Division of Publications

\$1.00 postpaid 6 x 9; 207 New York

CROSS-SECTIONS OF RURAL HEALTH

PROGRESS. *Report of the Commonwealth Fund Child Health Demonstration in Rutherford County, Tennessee, 1924-1928.*

By Harry S. Mustard.

The Commonwealth Fund Division of Publications

\$1.00 postpaid

New York

6 x 9; xiii + 230

Four attractively presented accounts of the Commonwealth Fund's health demonstrations in Oregon, Georgia, Tennessee, and North Dakota. As public health propaganda they are excellent. To our low commercial mind they are a trifle unsatisfying, because we are unable to find any very convincing evidence of tangible results. This is not to say that the demonstrations accomplished nothing; but merely (as is carefully stressed in each of these volumes) to point out that there is no satisfactory method of measuring what was accomplished.



FIFTY-TWO YEARS OF RESEARCH, OBSERVATION AND PUBLICATION

1877-1929. *A Life Adventure in Breadth and Depth. (With Complete Bibliography Chronologic and Classified by Subject 1877-1929.)*

By Henry F. Osborn. Charles Scribner's Sons

\$1.50 5 $\frac{3}{4}$ x 8 $\frac{1}{2}$; 160 New York

An autobiographic bibliography. The extent of Professor Osborn's labors and interests may be gauged by the fact that the chronological bibliography closes with number 801 (and there are more than 801 titles); and the classification by subject gives us the following:

Geology	12
Correlation, Zoogeography	10
Palaeontology	295
Zoology	31
Odontology and Odontography	11
Embryology	4
Neurology	9
Psychology	5
Anthropology	55
Evolution (Biology, Religion)	81
Eugenics (Heredity)	8
Education	58
Administration	78
Conservation	8
Biography	104
Miscellaneous	34



ILLUSTRATIONS AND PROOFS OF THE PRINCIPLES OF POPULATION. *Being the First Work on Population in the English Language Recommending Birth Control. Now Exactly Reproduced. With an Introduction Demonstrating Francis Place as the Founder of the Modern Birth Control Movement, Together with Unpublished Letters of Place on Birth Control, Coleridge's Criticisms of Malthus' Views on Birth Control.*

By Francis Place. *Critical and Textual Notes* by Norman E. Himes.

Houghton Mifflin Co.
Boston and New York

\$4.50

$\frac{1}{2} \times 8\frac{1}{2}$; 63 + xv + 355

Lowell, who liked

An old fashioned title-page, such as presents
A tabular view of the volume's contents,

would have been delighted with the title-page of this book, a photographic reproduction of an important but rare work. Place, while agreeing with Malthus as to the necessity for controlling the increase of population if the condition of the working classes were to be improved, concluded that Malthus' remedy of long-delayed marriage was impracticable and that

If, above all, it were once clearly understood, that it was not disreputable for married persons to avail

themselves of such precautionary means as would, without being injurious to health, or destructive of female delicacy, prevent conception, a sufficient check might at once be given to the increase of population beyond the means of subsistence; vice and misery, to a prodigious extent, might be removed from society, and the object of Mr. Malthus, Mr. Godwin, and of every philanthropic person, be promoted, by the increase of comfort, of intelligence, and of moral conduct, in the mass of the population.



SOIL. *Its Influence on the History of the United States. With Special Reference to Migration and the Scientific Study of Local History.*

By Archer B. Hulbert.

Yale University Press

\$2.50 6 x 9; xii + 227 New Haven

The writing of history has changed greatly since the days when it was merely a chronicle of wars and other political events. In spite of the jeremiads of die-hard historians of the old school, it has come to be recognized that politics are explicable only by considering the social and economic factors which underlie them, and that these in turn can be understood only in relation to man's environment. However, in this interpretation it has been mainly the topographic factors which have been emphasized, such as the influence of rivers and their valleys as means of communication and that of mountains as barriers. In this interesting book Mr. Hulbert takes up the hitherto neglected topic of the influence of soils on American settlement and expansion. As he points out, this is a subject which needs to be worked out in detail by local historians. The economic interpretation of history, although in some cases perhaps overworked, has been rich in results; we look forward to as abundant a harvest from its geological and biological interpretation.

PHYSICAL DIAGNOSIS.

By Warren P. Elmer and W. D. Rose.

The C. V. Mosby Co.

\$10.00 6 x 9; 903 St. Louis

Owing to the death of the author of this book Dr. Elmer was requested to revise the sixth edition. While much of the original subject matter has been retained there has been considerable change made in arrangement, a good deal of rewriting done and additions made to carry out the revisor's ideas. The book is now divided into two parts. Part I deals with the technic of physical examination and normal physical diagnosis; Part II with the physical diagnosis of disease. While designed primarily as a text-book for medical students, there are many aspects of this book which will be of great value to the physical anthropologist.



*THE MEASUREMENT OF MAN.

By J. A. Harris, C. M. Jackson, D. G. Paterson, R. E. Scammon.

University of Minnesota Press\$2.50 6 x 9 $\frac{1}{8}$; vii + 215 Minneapolis

Four lectures delivered under the auspices of Sigma Xi at the University of Minnesota. The late Professor Harris contributes illustrations of the various statistical techniques applicable to mass measurements. Professor Jackson writes on normal and abnormal human types; he is chiefly concerned with variation and correlation in body measurements. Professor Paterson, dealing with personality and physique, reviews the present state of our knowledge, with much valuable critical comment on the work that has been done. Professor Scammon, in the final paper, deals with the measurement of growth, and especially with the growth of the various parts and organs. We found this the most interesting chapter of the book.

SEVENTY BIRTH CONTROL CLINICS.
A Survey and Analysis Including the General Effects of Control on Size and Quality of Population.

By Caroline H. Robinson.

The Williams and Wilkins Co.\$4.00 5 $\frac{5}{8}$ x 8 $\frac{3}{8}$; xx + 351 Baltimore

Mrs. Robinson's book is intended to be a practical hand-book for those interested in the birth control movement. She has made a general survey of seventy organized centers located in the following countries: Germany, 16; Austria, 8; Russia, 1; Great Britain, 14; and the United States, 31. These furnish information on the

nature, extent, and status of this world-wide movement, insofar as these may be objectively determined by descriptions of leaders and workers, their policies, procedures, and experiences, the numbers of people reached, the expenses entailed, and the character and trend of public and professional opinion as reflected in laws and letters.

The book is in two parts; the first contains six chapters dealing with the survey, while the four chapters in the second part are concerned with social implications of birth control. The latter section contains much controversial material which the author frequently handles with a pleasant, if not always convincing assurance. The work includes much statistical data, a lengthy bibliography, an index and three appendices dealing with (a) Statistics of patients' social status, (b) Present and colonial fertility, (c) Additional centers for birth control. Dr. Robert L. Dickinson contributes a Foreword.

POPULATION (*Lectures on the Harris Foundation 1929*).

By Corrado Gini, Shiroshi Nasu, Robert R. Kuczynski, and Oliver E. Baker.

University of Chicago Press\$3.00 5 x 7 $\frac{1}{2}$; ix + 312 Chicago

In this series of lectures Professor Gini develops his concept of the nation as a superorganism with its periods of birth, growth, senescence and death, or in some cases rebirth; Professor Nasu discusses population and the food supply, with an interesting section on Japanese population problems; Dr. Baker treats the trend of agricultural production in North America, concluding that the great problem facing the American farmer will continue to be how to dispose of the surplus; and Dr. Kuczynski gives the reasons for his conclusion that the peoples of Western Europe and North America are close to a stationary condition.



THE MOUND-BUILDERS. *A Reconstruction of the Life of a Prehistoric American Race, Through Exploration and Interpretation of Their Earth Mounds, Their Burials, and Their Cultural Remains.*

By Henry C. Shetrone. D. Appleton and Co.
\$7.50 6 x 9½; xx + 508 New York

A highly interesting account of "the First American" written for the non-specialist. The author, curator of the museum containing the finest collection of relics of these early settlers, gives a remarkably clear picture of what investigations by archaeologists and anthropologists have produced. The numerous and well chosen illustrations add materially to the pleasure of reading the book. The bibliography contains general references on anthropology, the American Indian, archaeology of the Mound Area, and under headings of states where mounds have been studied, special references. There is an excellent index.



MENSCHEN DER VORZEIT. *Ein Überblick über die altsteinzeitlichen Menschenreste.*

By Hans Weinert. Ferdinand Enke Verlag
Rm. 8 (paper) Stuttgart
Rm. 9.50 (cloth)

6½ x 10; 139

A presentation, so far as possible in non-technical terms, of what is really known about paleolithic man, without attempts to embellish the subject with imaginary additions.



RASSENKUNDE DES JÜDISCHEN VOLKES.

By Hans F. R. Günther.

J. F. Lehmanns Verlag

11 marks (paper)

München

13 marks (cloth)

6 x 8½; 352

The kernel of this book was an appendix to the earlier editions of Dr. Günther's *Rassenkunde des deutschen Volkes*. His conclusion is that the Jews are not a race but a mixture of races.



ANCIENT EMIGRANTS. *A History of the Norse Settlements of Scotland.*

By A. W. Brøgger. Oxford University Press
\$5.00 5½ x 8¾; xi + 208 New York

Supplementing the scanty written records with evidence from place-names and archaeology, Dr. Brøgger attempts to reconstruct the history of the Norse settlements of the Orkneys and Shetlands.



ZOOLOGY

THE SALAMANDERS OF THE FAMILY PLETHODONTIDAE.

By Emmett R. Dunn. Smith College
\$6.00 Northampton, Mass.

6¼ x 9½; x + 441

To any person who shares the popular superstition that a taxonomist is not a human being, but merely a complex kind

of classifying machine, we recommend the reading of the Foreword to this book, with its vivid glimpses of places visited and adventures encountered in the quest for salamanders.

It has been thirteen years since the eighteen-year-old boy read those few words and in those thirteen years for him the surf has whitened the shores of Caribbean islands; the slopes of the Balsams have been blue in the distance; hawks have soared a thousand feet below the naked peak of Sharp Rock; the iridescent wings of Morpho have fluttered through glades in the rain forest and in the midst of the cataract at Xico; from the mooring at Vera Cruz tall Orizaba has stood against the western sky; the low sun has shone on the ice of Ixtaccihuatl, most unforgettable of mountains; step after step, for him, far out at sea, Chirripo Grande, "*nie von Menschenfuss betreten*," has climbed aloft; and from shaken Irazu, while the ash cloud of the eruption rose above his head and floated, a black pall beaten by the fierce wind, he has seen through a break in the clouds, far to the Southwards, the sheer and menacing shaft of rock which is Cerro de la Muerte.

So far as we can see, Dr. Dunn does not suffer as a taxonomist for being something of a poet as well: his monograph is a model of careful description and classification. We wish, however, that he would give us some day a fuller narrative of his adventures as a collector. It is an old and honorable form of naturalistic literature, and the book should be worth reading.



THE WILDERNESS OF DENALI. *Explorations of a Hunter-Naturalist in Northern Alaska.*

By Charles Sheldon. Charles Scribner's Sons \$6.00 6 $\frac{1}{8}$ x 9 $\frac{1}{8}$; xxv + 412 New York

The author of this entertaining account of a search for white or Dall sheep in the wildernesses of the region of Mt. McKinley died before his material was in final form for printing. This explains the wide gap in time between the years of exploration and hunting (1906-1908) and the recent date of publication. Readers of this

type of literature will derive much pleasure from the account of one who was not only a big game hunter but an explorer and naturalist as well. He has contributed many important facts concerning the habits and behavior of Alaskan mammals, especially those of the larger type, and in particular of the mountain sheep. The book is generously illustrated, contains temperature tables, lists of birds observed and mammals collected in the Denali region, localities in which the author hunted and tribes and bands visited. There is an excellent index and a map of the region explored. The explorer's wife contributes a preface and C. Hart Merriam an introduction. It is unfortunate that the picturesque name Denali, which the Indians gave the mountain, has not been retained.



THE WILD GRIZZLIES OF ALASKA.

A Story of the Grizzly and Big Brown Bears of Alaska, Their Habits, Manners and Characteristics, Together with Notes on Mountain Sheep and Caribou, Collected by the Author for the United States Biological Survey.

By John M. Holzworth. G. P. Putnam's Sons \$5.00 6 $\frac{1}{4}$ x 9 $\frac{1}{4}$; xxi + 417 New York

Mr. Holzworth is an experienced naturalist and a pioneer in motion picture photography of big game in North America. The first part of his book is a narrative of his adventures in photographing Alaskan bears; the second part is a description of the grizzly and brown bears, with a plea for their protection from extermination. The illustrations are superb. We can heartily recommend this book, both to those interested in bears and to those who like their adventure stories authentic as well as thrilling.



HUNTING THE ALASKA BROWN BEAR. *The Story of a Sportsman's Adven-*

ture in an Unknown Valley After the Largest Carnivorous Animal in the World.

By John W. Eddy. G. P. Putnam's Sons
\$3.50 6 x 8 $\frac{3}{4}$; xv + 253 New York

An account of a shooting expedition; not particularly interesting except to head and skin hunters. The illustrations of wild living bears and caribou were hardly worth including. There are some observations on the habits of the brown bear, but little of great value.



VERTEBRATE NATURAL HISTORY OF A SECTION OF NORTHERN CALIFORNIA THROUGH THE LASSEN PEAK REGION. *University of California Publications in Zoology* Volume 35.

By Joseph Grinnell, Joseph Dixon and Jean M. Linsdale.

University of California Press
\$6.00 Berkeley

7 x 10 $\frac{3}{4}$; v + 594 (paper)

This is the seventh in a series of surveys made by the California Museum of Zoology on vertebrate animal life in California. The "Lassen section" is in the northern part of California, where profound changes are taking place due chiefly to the invasion of man. The report includes records on the species and subspecies of land vertebrates found; the frequency of observed occurrence and the relative abundance of these kinds; the local or habitat distribution of each kind; factors determining distribution, etc. The work is abundantly illustrated, chiefly with photographs, contains a list of references and is indexed.



THE AFRICAN REPUBLIC OF LIBERIA AND THE BELGIAN CONGO. *Based on the Observations Made and Material Col-*

lected During the Harvard African Expedition, 1926-1927. Vols. I and II.

Edited by Richard P. Strong.

Harvard University Press
\$15.00 a set Cambridge

7 $\frac{1}{2}$ x 10 $\frac{3}{8}$; xxxv + 1064

Two large and handsome volumes on the results of the Harvard African Expedition of 1926-27, which contain material of interest to students of many branches of science. Part I of Volume I contains an account of Liberia and its natives; Parts II and III deal with medical, pathological, and biological investigations. Volume II contains the zoological results of the expedition.



EXPERIMENTAL-ZOOLOGIE. 7.

ZOOTECNIKEN. *Eine Zusammenfassung der für Versuche mit Tieren Verfügbaren Forschungsweisen. (Fragestellung, Versuchsführung, Bearbeitung).*

By Hans Przibram.

30 marks (paper)

45 marks (bound)

7 x 10 $\frac{1}{4}$; viii + 269 + 10 plates (paper)

The concluding volume of this work deals with the technique of experimental zoology. The three sections deal with preparation for experiment, the actual experimental work, and the preparation of the results for publication. There is much valuable advice on all sorts of subjects; not the least valuable are the chapters on sources of errors.



HISTOLOGICAL AND ILLUSTRATIVE METHODS FOR ENTOMOLOGISTS.

By H. Eltringham (*With a chapter on mounting whole insects by H. Britten*).

Oxford University Press
\$2.50 4 $\frac{3}{4}$ x 7 $\frac{1}{8}$; xii + 139 New York

A useful addition to the literature of laboratory technique.

This little handbook does not aspire to be a textbook of Invertebrate Histological Technique. Indeed the subject can hardly be regarded as sufficiently advanced for the production of a volume in any way comparable to the available manuals on the staining and preparation of vertebrate tissues. It is rather an attempt to describe, for the use of those who have not had the advantage of laboratory training, the more elementary methods of entomological section-cutting and staining together with hints on other processes of microscopic entomology.



INVESTIGATIONS ON PLANKTON PRODUCTION IN FISH PONDS. *Bureau of Fisheries Document No. 1082*

By A. H. Wiebe.

U. S. Government Printing Office
15 cents $7\frac{1}{2} \times 11$; 40 (paper) Washington

An account of experiments to determine the factors involved in the use of fertilizers to increase the production of plankton as food supply for fish. Soluble phosphorus is sometimes a limiting factor, but apparently there are also other limiting factors, as yet not identified.



THE STUDY OF BIRDS. *An Introduction to Ornithology.*

By E. M. Nicholson.

Jonathan Cape and Harrison Smith
60 cents $4\frac{1}{2} \times 6\frac{3}{4}$; 125 New York

The purpose of this little book is to outline "the principal methods by which ornithology is at present proceeding, and the problems which it is solving, or hopes to solve in the future." It will be of interest to amateur naturalists and to members of ornithological clubs.



HANDBUCH DER BIOLOGISCHEN ARBEITSMETHODEN. *Lieferung 338.*

Containing following articles: *Die pH-Bestimmung mit dem Hydrionometer*, by Ernst Bresslau; *Haltung und Aufzucht von Süßwasserschwämmen*, by Kurt Schröder; *Fang, Pflege und Zucht der deutschen Süßwasseregeln*, by Konrad Herter.

Urban und Schwarzenberg

4 marks 7×10 ; 68 (paper) Berlin

This number of the *Abderhalden Handbuch* contains a good discussion of the laboratory husbandry of fresh-water sponges and leeches.



COSTUMBRES DE INSECTOS. *Observadas en Plena Naturaleza.* Tomo I. Tomo II.

By P. Eugenio Sáez, S. J. *Revista Ibérica*
2 ptas. each Barcelona

$6 \times 8\frac{1}{2}$; Tomo I, 103 (paper)

Tomo II, 95 (paper)

In these volumes a Spanish Father Wassmann records his observations on insects and applies them *ad maiorem Dei gloriam*.



CILIATES FROM BOS INDICUS LINN. I. *The Genus Entodinium Stein.* *University of California Publications in Zoology*, Vol. 33, No. 22.

By Charles A. Kofoed and Ronald F. MacLennan.

\$1.00 $7 \times 10\frac{3}{4}$; 74 + 4 plates (paper)

THE MORPHOLOGY, TRANSMISSION, AND LIFE-HISTORY OF HAEMOPROTEUS LOPHORTYX O'ROKE, A BLOOD PARASITE OF THE CALIFORNIA VALLEY QUAIL. *University of California Publications in Zoology*, Vol. 36, No. 1.

By Earl C. O'Roke.

University of California Press

65 cents

Berkeley

$7 \times 10\frac{3}{4}$; 50 + 2 plates (paper)



BOTANY

MOLDS, YEASTS, AND ACTINOMYCETES. *A Handbook for Students of Bacteriology.*

By Arthur T. Henrici.

John Wiley and Sons, Inc.

\$3.50 $5\frac{3}{4} \times 9\frac{1}{8}$; x + 296 New York

A book of great usefulness to students and investigators. Molds, yeasts, and

actinomycetes cause diseases in man and animals; chemical transformations of the soil; and contamination of food. They are valuably employed in a wide variety of industries and in the future will probably be more so. These considerations lead the author to the view that these organisms require a more extensive general treatment than has hitherto been accorded them. The present volume is the outgrowth of a course of lectures given at the University of Minnesota to advanced students whose future work was to be in bacteriology. The author therefore deals equally with the medical and industrial aspects of the subject. The treatment is such that students, and bacteriologists in particular, can easily use the more technical literature. The book is generously illustrated. The keys are not too detailed but sufficient for advanced work. Literature lists accompany each chapter and there are author and subject indices.



EXPLORING FOR PLANTS. *From Notes of the Allison Vincent Armour Expeditions for the United States Department of Agriculture, 1925, 1926, and 1927.*

By David Fairchild. The Macmillan Co.
\$5.00 6 x 9 $\frac{1}{4}$; xx + 591 New York

The author of this delightful book has succeeded in conveying to the reader much of the excitement and pleasure which he experienced in his search for plants in foreign lands. As a special agricultural explorer of the Office of Foreign Plant Introduction of the United States Department of Agriculture, Dr. Fairchild searches for rare and useful plants that can be introduced into the United States either for the purpose of improving existing strains or to increase our useful and ornamental varieties. Algeria, Morocco, the west coast of Africa, Ceylon, Sumatra and Java were his hunting grounds in this volume.

In many of the regions visited he found much material in botanic gardens. These ranged from small private jungle gardens to the formal and very beautiful Peradeniya garden in Ceylon, established by the British in 1821. Much of the collecting, however, was in the wild. It was inevitable that there should be many unique experiences which the ordinary traveller in the orient misses, but throughout the book the reader's main interest is linked with the author's in the search for new and interesting plants. The book is abundantly illustrated with photographs taken on the expeditions. There is an index.



THE GREEN LEAF. *The Major Activities of Plants in Sunlight.*

By D. T. MacDougal. D. Appleton and Co.
\$2.00 5 x 7 $\frac{1}{2}$; iv + 142 New York

Among the most promising of the series of books on science for the general reader which have been appearing lately is Appleton's *New World of Science* Series. This was inaugurated by Heyl's excellent *New Frontiers of Physics*, one of the most lucid accounts that we have read of the subject, and also includes Taylor's *Antarctic Adventure and Research*, already noticed in these columns, and Koppanyi's *The Conquest of Life*. The present book deals with plant physiology, a subject about which most of us know much less than about animal physiology. We can heartily recommend it to all those who like their popular science to be accurate as well as picturesque.



OUR PLANT FRIENDS AND FOES.

By William A. DuRoi.

The John C. Winston Co.
\$1.00 5 $\frac{1}{4}$ x 7 $\frac{1}{4}$; xiv + 277 Philadelphia

An entertaining and instructive book for the amateur. There is much in it that

is common knowledge to the student and the investigator but is not usually recounted for the layman in non-technical language. We read that tomatoes grow on poisonous plants; that although bamboo grows to be 100 feet tall, it is a grass; that the apple tree is an overgrown rose bush, that the development of the sugar beet industry goes back to the Napoleonic Wars when Napoleon ordered French investigators to find a substitute for sugar cane, etc., etc. There is a very clear exposition of the manufacturing of sugar by green leaves. Great care has been taken to make the book authentic. It is well illustrated but is without index.



STRASBURGER'S TEXT-BOOK OF BOTANY. *Sixth English Edition.*

Rewritten by Hans Fitting, Richard Harder, Hermann Sierp, George Karsten. Translated from the Seventeenth German Edition by W. H. Lang.

The Macmillan Co.

\$9.00 $5\frac{3}{4} \times 8\frac{1}{2}$; xi + 799 New York

The first edition of this widely used text book first appeared in 1894. Since then it has gone through many editions, both in German and in English, and there have been extensive changes made involving complete rewriting. The original authors no longer appear on the title page and only the founder's name has been preserved in the title. In the present edition the section on *Morphology* is by Fitting; that on *Physiology* by Sierp; that on *Thallophyta*, *Bryophyta*, and *Pteridophyta* by Harder; and that on *Spermatophyta* by Karsten.



A TEXTBOOK OF PLANT PHYSIOLOGY.

By N. A. Maximov (Translated from the Russian. Edited by A. E. Murneck and R. B. Harvey). McGraw-Hill Book Co., Inc.

\$4.00 $5\frac{3}{4} \times 9$; xvi + 381 New York

A welcome addition to text and refer-

ence books in plant physiology. The author, director of plant physiological work in the Institute of Applied Botany of the Soviet Government, is outstanding for his work on temperature, light and water relations in plants. The book is well arranged for teaching. Frequent use has been made of American contributions, but the chief feature of the book is the opportunity which it offers to those who do not read Russian to become familiar with important researches, particularly on cold and drouth resistance, which the author has made his particular field. The illustrations are excellent and well chosen. There is a bibliography of English titles and an index.

The translation has been made with much care. All corrections which are to be incorporated in the forthcoming second Russian edition appear in this issue.



PLANT PHYSIOLOGICAL CHEMISTRY.

By Rodney B. Harvey. The Century Co.

\$6.00 $5\frac{3}{4} \times 8\frac{3}{4}$; xix + 413 New York

A text book on the physiological chemical mechanism of plants. The main headings are: Introduction; General metabolism; Carbohydrates; Fats, phosphatides, and waxes; Proteins; Photosynthesis; Respiration. There are practically no references to the literature in the text, but a bibliography of twenty-two pages is appended.



THE LOWER FUNGI. *Phycomycetes.*

By Harry M. Fitzpatrick.

McGraw-Hill Book Co., Inc.

\$4.00 $5\frac{3}{4} \times 9$; xi + 331 New York

This book will serve as a text-book or reference work for beginning and advanced students. It has been designed also to provide a comprehensive treatment of the taxonomy and morphology of the Phyco-

mycetes for the research worker. The book is copiously illustrated and contains keys to all the genera. Literature lists, frequently lengthy, are included in each section. There is an index.



GENERAL ELEMENTARY BOTANY.
With Practical Applications. Revised Edition.

By Elmer Campbell. Thomas Y. Crowell Co.
\$3.00 5½ x 8½; xiii + 410 New York



MORPHOLOGY

LEONARDO DA VINCI THE ANATOMIST (1452-1519).

By J. Playfair McMurrich.

Published for Carnegie Institution of Washington by The Williams and Wilkins Co.

\$6.00 6⅞ x 9⅞; xx + 265 Baltimore

This beautiful volume reflects great credit upon its author; upon his sponsor, the Carnegie Institution of Washington; and upon its publisher. It is a full-length portrait of Leonardo as a biologist. It is equally characterized by literary charm and sound, penetrating scholarship. Once more it brings evidence of the rightness of the thesis we have before maintained in these columns, that the professional scientific man is apt to become a more effective historian of his subject than is the professional historian who turns to science for material with which to exercise his pen and his scholarship.

The first six chapters lay the historical background for the discussion of Leonardo's anatomical work. The next twelve chapters take up the details of that work, by organ systems. These are followed by three chapters on embryology, comparative anatomy and botany, respectively, while a short final chapter of conclusions brings the text to an end. There is a bibli-

ography and a detailed index. The volume is abundantly and well illustrated.

McMurrich accords Leonardo a high place as an anatomist, which would have been higher had his work been published. He says: "Vesalius was undoubtedly the founder of modern anatomy—Leonardo was his forerunner, a St. John crying in the wilderness."



CONTRIBUTIONS TO EMBRYOLOGY.
Volume XXI, Nos. 118 to 125. Carnegie Institution of Washington Publication No. 407. Containing following articles: *A Human Embryo with Seventeen Pairs of Somites*, by Wayne J. Atwell; *Description of a Human Embryo of Eight Somites*, by Cecil M. West; *Medullated Tracts in the Brain Stem of a Seventh-Month Fetus*, by O. R. Langworthy; *Ossification of the Otic Capsule in Human Fetuses*, by T. H. Bast; *On an Unusual Placental Form in the Hyracoidea; Its Bearing on the Theory of the Phylogeny of the Placenta*, by George B. Wislocki; *Gross and Microscopic Structure of Thyroid Gland in Man*, by W. F. Rienhoff, Jr.; *The Age Factor in Grafts*, by Vera Danchakoff and V. E. Danchakoff; *The Early Embryology of the Rabbit*, by P. W. Gregory.

Carnegie Institution of Washington
\$6.00 (paper) Washington
\$7.00 (cloth)

9½ x 11½; 168 + 29 plates

Another volume of these contributions, which maintains, both in matter and in form, the high standard set by previous volumes.



STUDIES ON THE STRUCTURE AND DEVELOPMENT OF VERTEBRATES.

By Edwin S. Goodrich. The Macmillan Co.
\$10.00 5⅝ x 8½; xxx + 837 New York

A careful and useful treatise on some problems of vertebrate morphology. The chapter headings indicate the scope of the

work: Vertebral column, ribs and sternum; Median fins; Paired limbs; Limb girdles; Morphology of head region; The skull; Skeletal visceral arches and labial cartilages; Middle ear and ear ossicles; Visceral clefts and gills; Vascular system and heart; Air-bladder and lungs; Subdivisions of the coelum, and diaphragm; Excretory organs and genital ducts; Peripheral nervous system and sense organs. The illustrations are numerous and excellent; over 300 out of 754 are new. There is a classification scheme of 16 pages; a bibliography of 1186 titles, and a good index. A sound and valuable work.

A TEXT-BOOK OF HISTOLOGY.

By Alexander A. Maximow. Completed and edited by William Bloom.

W. B. Saunders Co.

\$9.00 $6\frac{1}{2} \times 9\frac{3}{4}$; xiii + 833 Philadelphia

It was Professor Maximow's plan to write a text-book based, so far as possible, on human material. At the time of his death he had entirely completed the sections on the male and female generative organs, the urinary tract, the organs of special sense, and epithelium. Others, on the blood and connective tissue, the gastrointestinal tract, the blood vascular and lymphatic systems, the spleen, the integument, and the mammary gland, were in rough manuscript. The difficult task of completing the book fell to Professor Bloom. This he has done with careful regard to Professor Maximow's original plan. The sections on the biliary and respiratory systems, the pancreas, and the endocrine glands, and also the introductory chapter, have been written by him, and he has revised and completed those parts that were in rough draft. Professor Herrick is chiefly responsible for the section on the nervous tissue.

The illustrations are numerous and ex-

cellent, the references are few but have been carefully selected. There is a detailed index. Teachers of histology will find this an excellent text-book. It should be among the reference books in all biological laboratories.

THE ANATOMY OF THE HUMAN BODY. *Twenty-second Edition.*

By Henry Gray (Thoroughly Revised and Re-edited by Warren H. Lewis).

Lea and Febiger

\$10.00 $6\frac{1}{2} \times 10\frac{1}{8}$; 1391 Philadelphia

While the latest edition of this classic text has been brought up to date by incorporating new anatomical knowledge and by a thorough revision of the section on the central nervous system, "the plan originally formulated, which has proved so successful, has been adhered to as much as possible."

A TEXT-BOOK OF HISTOLOGY.

By Harvey E. Jordan. D. Appleton and Co.

\$7.00 $6 \times 8\frac{1}{2}$; xxviii + 857 New York

The fifth edition of this excellent text has been thoroughly revised and added to, especially in the chapters on blood and the endocrine tissues.

DEVELOPMENTAL ANATOMY. *A Text-Book and Laboratory Manual of Embryology. Second Edition. Reset.*

By Leslie B. Arey. W. B. Saunders Co.

\$6.50 $6\frac{1}{2} \times 9\frac{3}{4}$; ix + 563 Philadelphia

GRUNDZÜGE DER ENTWICKLUNGSGESCHICHTE DES MENSCHEN *in vergleichender Darstellung. 12. neubearbeitete und wesentlich erweiterte Auflage.*

By Richard Weissenberg. Georg Thieme

15 marks Leipzig

$5 \times 7\frac{3}{4}$; xv + 437 + 6 plates

PHYSIOLOGY AND PATHOLOGY

THE STORY OF A SURGEON.

By Sir John Bland-Sutton.

Houghton Mifflin Co.
Boston and New York

\$3.50 $5\frac{1}{2} \times 8\frac{3}{4}$; xii + 204

Sir John Bland-Sutton is one of the most picturesque figures in the medical world. To an extraordinary degree he has kept undiminished, throughout a long and distinguished career as a surgeon, that naive intellectual curiosity and wide-ranging interest in literally everything, which is commonly found in a bright and keen boy, but almost never in a man of 76 loaded with honors and professional and social responsibilities. This autobiography is a delightful book. One's only regret is that it is not twice as long. As those who know him personally are aware, and as is reflected in this book as well as in all his other writings, Sir John's store of odd and curious information, especially about zoological matters, is simply amazing. Zoology was his first love, and he has always been faithful to it. He says (p. 178):

Zoology is omnipotent among sciences and it is the oldest study in the world. We become familiar with it in the nursery, and our interest in it increases with our religious exercises. Eden was the first Zoological Gardens and Adam had the privilege of naming animals unfettered by priority of nomenclature which is the bugbear of learned zoologists. The Bible opens with a delightful jungle story: Eden—a jungle—where our first parents wandered in perfect happiness until they were disturbed by an Evil Spirit in the form of a wily snake under an apple-tree, and Eve, wishful for a change of diet, ate an apple, lost Eden and brought Sin and Death into the world.

Every biologist should read this book. It will stimulate as well as entertain him. It is copiously illustrated, including some examples of Sir John's own skill as a draughtsman—he says that he learned to

draw by watching pavement artists. Unfortunately there is no index.



NERVOUS INDIGESTION.

By Walter C. Alvarez. Paul B. Hoeber, Inc.

\$3.75 $5\frac{1}{2} \times 8\frac{1}{8}$; xvi + 297 New York

To the general practitioner this book will be invaluable. Much common sense and sage advice are to be found within its pages. The author is on the staff of the Mayo Clinic. He is a physician of wide experience in the handling of nervous patients and has an unusually keen appreciation of the difficulties which beset the person with functional disorders of the digestive tract as well as the difficulties which confront the physician in treating these disorders. The subjects discussed are: Ways in which emotion can affect the digestive tract; Types of indigestion; Hints in regard to the taking of a history; The handling of the nervous patient; The treatment of nervous indigestion; Some practical points about the physiology and innervation of the digestive tract; Suggestions for further reading. In the preface Dr. Alvarez makes a plea for a more extensive training of the medical student in the treatment of the nervous patient. The book is well documented and indexed.



A TEXT-BOOK OF PHYSIOLOGY for Medical Students and Physicians. Eleventh Edition. Thoroughly Revised.

By William H. Howell.

W. B. Saunders Co.

\$6.50 $5\frac{3}{4} \times 9\frac{1}{8}$; 1099 Philadelphia

In the latest revision of this standard text-book Dr. Howell follows his previous policy of selection rather than condensation, of treating the more important subjects in sufficient detail to give the student a serviceable conception of the facts, in-

stead of attempting a more summary treatment of a larger number of topics.

Everything that can be ascertained in regard to the general physiology of the cell is of fundamental importance to the student of physiology, because in the long run explanations of the phenomena exhibited by living things must rest upon these basic properties, but we must recognize that in the multicellular organisms differentiation in function and the mutual dependence and interaction of the various tissues, in carrying out the reactions of the complex structure considered as a whole, have given rise to numerous delicately balanced mechanisms that are of essential importance for the maintenance of the integrity of the organism. The immediate need of the medical student is to become conversant with these mechanisms as far as they are known, and, perhaps, the first duty of a text-book in physiology is to give the necessary information as clearly and accurately as possible.

In this sense a text-book of animal physiology is still largely descriptive in its treatment, although as our knowledge becomes more exact and more comprehensive mere description is being replaced or supplemented in large measure by expositions of fundamental principles.



EDWARD JENNER *and the Discovery of Smallpox Vaccination.*

By Louis H. Roddis. George Banta Publishing Co.

\$1.00 5 x 7; iv + 155 Menasha, Wis.

Although a small book there is much interesting material to be found within these pages. Jenner led a busy life as a country practitioner but he had many other interests than healing the sick. Music gave him great pleasure, he sometimes composed verse, also he devoted considerable time to the study of natural history, being especially interested in the migratory habits of British birds. The author gives a graphic description of Jenner's work on small pox and of the interest and antagonism which it aroused among practitioners and laymen. Many of Jenner's letters and those of his correspondents are included in the text and several interesting documents among which

are "Some accounts of the success of inoculation for the small pox in England and America," by Benjamin Franklin; "Plain instructions for inoculation in the small pox," by William Heberden, and William Cobbett's diatribe on vaccination. The work concludes with a list of 32 important contemporary books and documents referring to small pox, a list of Jenner's published writings and an appendix in which are included reports of various vaccination commissions, mortality tables, etc.



PHYSIOLOGY.

By John F. Fulton. Paul B. Hoeber, Inc.
\$1.50 4 $\frac{1}{4}$ x 6 $\frac{5}{8}$; xvi + 141 New York

An excellent addition to the *Clio Medica* series of historical primers published by Paul Hoeber. In five chapters and an Epilogue, the author, who has recently become Stirling Professor of Physiology in Yale University, discusses Aristotle and Galen; the circulation of the blood; respiration; digestion; physiology in the nineteenth century and the rise of teaching laboratories; and the trend of modern physiology. Having regard to the limitations imposed by its size it seems to us to be the best history of physiology yet written. There is a good bibliography and thorough indexes.



AN INTRODUCTION TO HUMAN EXPERIMENTAL PHYSIOLOGY.

By F. W. Lamb. Longmans, Green and Co.
\$4.00 5 $\frac{3}{8}$ x 8 $\frac{1}{2}$; xii + 335 New York

Undoubtedly the study of physiology with the student himself or his fellow-student as the subject of investigation has much to commend it. In this book is presented "the class experiments on blood, respiration, and circulation, and in some sections more advanced work, together

with remarks on the problems to which the methods have been applied by various workers." The book is well documented and indexed.



ALIMENTARY ANAPHYLAXIS (*Gastro-intestinal Food Allergy*).

By Guy Laroche, Charles Richet Fils and François Saint-Girons. Foreword by Charles Richet. Translated by Mildred P. Rowe and Albert H. Rowe.

University of California Press

\$2.00 postpaid 5 x 7; 139 Berkeley

Many interesting facts are brought out in this little book indicating the importance and need of further research into the causes, symptoms and treatment of food allergy. The authors believe that all foods, except water and sugar, and most chemical products may produce an anaphylactic state. The discussion of the experimental work relates almost entirely to that of European investigators. There is no mention of the work in skin reactions, which is essentially an American contribution. One of the translators contributes a preface to the American edition. There is a bibliography of over 100 titles but no index.



ARTIFICIAL SUNLIGHT. *Combining Radiation for Health with Light for Vision.*

By M. Luckiesh.

D. Van Nostrand Co., Inc.

\$3.75 6 x 9; 254 New York

A treatise on the artificial production of the various forms of radiation found in sunlight. There is a considerable amount of technical data which will be useful to anyone who desires to do experimental work on the biological aspects of radiation.

HANDBUCH DER BIOLOGISCHEN ARBEITSMETHODEN. *Lieferung 331. Methoden und Technik der vergleichenden Stoffwechselphysiologie bei Wirbellosen.*

By H. P. Wolvekamp.

Urban und Schwarzenberg

5.50 marks 7 x 10; 86 (paper) Berlin
HANDBUCH DER BIOLOGISCHEN ARBEITSMETHODEN. *Lieferung 332. Methoden zur Untersuchung des Verwendungsstoffwechsels pathogener Bakterien.*

By Hugo Braun Urban und Schwarzenberg

4.20 marks 7 x 10; 78 (paper) Berlin
HANDBUCH DER BIOLOGISCHEN ARBEITSMETHODEN. *Lieferung 341.*

Containing following articles: *Die radio-metrische Mikroanalyse*, by Rudolf Ehrenberg; *Eine Methode zur Beobachtung lebender Organe mit stärksten Vergrößerungen im Lumineszenzlicht (Intravitalmikroskopie)*, by Philipp Ellinger and August Hirt; *Die Methoden der elektrischen Kurzwellenanwendung*, by Erwin Schliephake; *Methodik der Messung kurzschenkelliger Winkel an biologischen Objekten*, by Paul Weiss.

Urban und Schwarzenberg

9 marks 7 x 10; 112 (paper) Berlin

These numbers of the Abderhalden *Handbuch* are of interest to physiologists. Number 331, which completes the volume on the comparative physiology of invertebrates, and deals with invertebrate metabolism, will be of general interest.



CLINICAL AND EXPERIMENTAL EXAMINATIONS IN PATIENTS SUFFERING FROM MB. MENIÈRI INCLUDING A STUDY OF THE PROBLEM OF BONE-CONDUCTION. (In two volumes).

Acta Oto-Laryngologica. Supplementum X, XI.

By Dida Dederding

Mercators Tryckeri Aktiebolag, Finland

(May be obtained through The

Editor, Sabbatsbergs Sjukhus,
Stockholm)

25 Swedish crowns per volume

(4 fascicles)

6 $\frac{3}{8}$ x 9 $\frac{1}{2}$; No. I, 156

No. II, 213 (paper)

An investigation of 135 patients in the Municipal Hospital of Copenhagen, with full clinical and experimental details. "Mb. Menièri" is the disease which has as one of its symptoms a continuous ringing in the ears. Martin Luther is supposed to have had it. Indeed it has been alleged to have been the cause of some of the sourer elements of his theology.



BIOCHEMISTRY

ENZYMES.

By J. B. S. Haldane.

Longmans, Green and Co.

\$5.50 6 x 9 $\frac{1}{2}$; vii + 235 New York

This book is based on a course of lectures which the author has been giving in the University of Cambridge for the last seven years. There has been no attempt to present a comprehensive treatise on the subject, the author having limited himself to an account of the purely chemical side of enzymes. It is necessary that the reader have a considerable knowledge of organic and physical chemistry. After a brief introduction enzymes are discussed under the following headings: The influence of enzyme concentration and hydrogen ion concentration; The union of the enzyme with its substrate and related compounds; The influence of temperature and radiation on enzyme action; The course of enzymatic reactions, and its mathematical theory; Specificity; Coenzymes, activators, kinases, and complements; The poisoning of enzymes; The purification and

chemical nature of enzymes; Theories of enzyme action, and classification of enzymes. There is appended to Chapter VI a brief section on recent work in carbohydrate chemistry. The book is well documented, and maintains the high standard of quality associated with the series in which it appears.



HANDBUCH DER BIOLOGISCHEN ARBEITSMETHODEN. *Lieferung 336. Die Verseifung.*

By Franz Bachér. Urban und Schwarzenberg
16 marks 7 x 10; 294 (paper) Berlin

HANDBUCH DER BIOLOGISCHEN ARBEITSMETHODEN. *Lieferung 339.*

Neuere Synthesen biologisch wichtiger Pyridinkörper.

By Hans Horsters and Helene Horsters.

Urban und Schwarzenberg

5 marks 7 x 10; 92 (paper) Berlin

These two numbers of the Abderhalden *Handbuch* on saponification and on the synthesis of pyridine compounds will be of interest to biochemists.



SPIRAZINES. *A Type of Chemical Structure Bearing Upon the Constitution of Proteins and the Cause of Life.*

By Carl F. Krafft.

Carl F. Krafft

50 cents

Box, 1421, Washington, D. C.

5 x 7; 54

Mr. Krafft suggests that the growth and division of cells may be explained by a spiral arrangement of atoms in the protein molecules, in place of the familiar ring. The idea is ingenious but it does not seem to have found favor with the biochemical journals.

SEX

THE DEVELOPMENT OF SEX IN VERTEBRATES.

By F. W. Rogers Brambell (with a Preface by Julian S. Huxley).

The Macmillan Co.

\$4.00 $5\frac{3}{8} \times 8\frac{1}{2}$; xvi + 261 New York

The author has endeavored to bring together and correlate recent work on the development of sex, both from the morphological and physiological side, and from the genetic and cytological. The book is, taken as a whole, an excellent piece of work, and one that will provide a good survey of the present state of our knowledge. The chapter headings indicate the scope of the work: Reproduction in Vertebrates; Spermatogenesis; Oogenesis and Fertilisation; The Sex Chromosomes; The Sex-ratio; The Origin of the Primordial Germ-cells and the Formation of the Germinal Ridges; The Differentiation of Sex and the Development of the Gonads; The Ovarian Follicle; The Corpus Luteum; Hermaphroditism; Sex-reversal in Fish and Amphibia; Sex-reversal in Birds; Gynandromorphism and the Control of the Sexual Characters; Conclusion.

We must point out, however, one sentence: "It may be concluded that the study of the mammalian sex-ratio, probably the oldest method of attacking the problem of sex-determination, thus provides weighty evidence in favour of the sex-chromosome theory."

This sentence seems to us one of the worst examples of faulty reasoning we have recently seen. Actually, no solitary piece of evidence offered in the chapter on the sex ratio can be used in support of the sex-chromosome theory; every one, without exception, requires some additional *ad hoc* hypothesis to reconcile it with the theoretical consequences of the sex-chromosome theory. We do not argue

that the theory is unsound; but we object to bad logic, and perhaps most strongly when it is used to support a good theory.



BIOMETRY

BARLOW'S TABLES of Squares, Cubes, Square Roots, Cube Roots, and Reciprocals of All Integer Numbers up to 10,000. Third Edition.

Edited by L. J. Comrie.

E. and F. N. Spon, Ltd.

7 s. 6 d. net

London

$5\frac{3}{8} \times 8\frac{1}{2}$; xii + 208

Since 1840, when De Morgan edited a new edition of Barlow's Tables, successive reprints of this useful work have been printed from the same stereotype plates. As these, after ninety years of service, have begun to show wear, the publishers, in resetting the book, have taken the opportunity to introduce various improvements, such as interlinear differences and a column of $\sqrt{10n}$ to give the user the benefit of a four-figure argument in all extractions of a square root. Moreover, the tables of powers higher than the cube in the original edition of 1814, which were omitted in 1840, have been restored. With these improvements Barlow may look forward to another ninety years of usefulness to the quantitatively minded.



PSYCHOLOGY AND BEHAVIOR

THE PRINCIPLES OF PSYCHOPHYSIOLOGY. A Survey of Modern Scientific Psychology. Volume II. Sensation.

By Leonard T. Troland.

D. Van Nostrand Co.

\$4.00 $5\frac{1}{4} \times 8\frac{1}{2}$; xxi + 397 New York

This is the second of four volumes planned to constitute a thorough treatment

of physiological psychology. The first volume deals with the definition of psychology, the methods of psychology, and perception; the latter subject being used to furnish a concrete and somewhat simple example of psychophysiological methods. The second volume concerns sensation, defined by the author as "the relationship between consciousness and processes in the afferent nervous arc, including the sense-organs and their immediate stimuli." The third volume is to be confined to a discussion of cerebration and action, while the fourth volume will consider the philosophical developments which arise from psychophysiology. Each one of the four volumes is so arranged that it can be read and used as a textbook without a knowledge of the other three.

Volume II, which deals with sensation, is

concerned with the indirect relationships between consciousness and the so-called "afferent arc" or the sector of the nerve conduction path which starts with the sense-organ stimulus and ends at the sensory projection areas of the cerebral cortex.

In this study the author has brought together all the available knowledge from physiology and applied it to psychology. In the first chapter on the Concept of Sensation, a physiological interpretation of neural activity is clearly and thoroughly presented; the remaining chapters deal with visual sensation, auditory sensation, the chemical senses, the cutaneous senses, and kinaesthetic and internal sensations.

The author is of the opinion that advance in psychological theory will come only through a knowledge of the facts of psychophysiology; he discards extreme behaviorism as being worthless, and holds that introspective psychology is only of *value* when correlated with the facts which behaviorists are emphasizing. He also believes that the positive propositions of

the *Gestalt* and structural psychologies are in general correct.

The book will make an excellent textbook for psychology students, because it will compel them to have a certain much-needed respect for physiology.



SOCIAL PSYCHOLOGY. *An Analysis of Social Behavior.*

By Kimball Young. F. S. Crofts and Co. \$4.00 6 x 9 $\frac{1}{4}$; xxxviii + 674 New York

One of the most frequent criticisms of science is that, while it has vastly increased our control of the external world, it has given us little aid in controlling ourselves, either as individuals or as groups, that it has invented edged tools for our use but has not taught us how to use them without cutting ourselves. The most promising answer to this criticism seems to be the new science of social psychology, with which Dr. Young deals in this book. It is his contention that in the still somewhat embryonic stage of development of the subject the descriptive method is, on the whole, the most appropriate, leaving quantitative treatment and generalization for later workers. His book therefore uses the case study method extensively.



HUMANISTIC LOGIC FOR THE MIND IN ACTION.

By Oliver L. Reiser. Thomas Y. Crowell Co. \$3.00 5 $\frac{1}{2}$ x 8 $\frac{1}{2}$; x + 326 New York

The author's *apologia* is:

This book aims at being something more than just another logic text. It attempts to broaden the scope of logic by relating the reasoning process to other human activities. The purpose of a course in logic is not conceived to be that of making human beings over into purely intellectual reasoning machines. The function of thought is held to be that of coordinating responses, of integrating human interests. It is held, therefore, that the function of a course in logic consists in showing individuals how to achieve a measure

of intellectual synthesis, a unity of insight and outlook, in a world which is rapidly changing in its physical and social aspects.

The present volume is written under the definite conviction that before the logician can make persons logical he must get them interested in being as intelligent and as intellectually honest as they can be. Hence the first two parts of the book consist in an attempt to "humanize" logic, to relate it to the broader adventure of living in the modern world.

Dr. Reiser seems to us to have succeeded admirably in his aim. On some of the topics much more might have been said, but the book is an excellent introduction to logic from a biological and humanistic point of view.

BEHAVIORISM. *A Battle Line.*

Edited by William P. King.

Cokesbury Press
\$2.25 5½ x 8; 376 Nashville, Tenn.

Now that evolution has been put down, the next Holy War is evidently to be against behaviorism. On the jacket of this book we are warned that

Behaviorism in science and humanism in philosophy are the twin modern foes of religious faith.

In "Behaviorism: A Battle Line" representatives of Protestant, Catholic, and Jewish faiths take a common position against materialistic behaviorism. These noted clergymen, philosophers, editors, and psychologists make a merciless exposure of the errors of the new psychology both in theory and practice.

This book will awaken many to the danger that threatens. It will fortify them against the attack of the materialist who expresses the presumptuous purpose of destroying all religious faith.

A Cokesbury Good Book

However, the contents of the book are not nearly so dreadful as one might anticipate from this Encyclical, being devoted mainly to a criticism of the curious self-denying ordinance by which really devout behaviorists renounce the opportunity to peek behind the scenes of human behavior. We find little in it that has not been as well said before this.

MORAL SENSE.

By James Bonar. The Macmillan Co.

\$4.00 5½ x 8½; 304 New York

In this volume of the Library of Philosophy, Dr. Bonar, the author of *Malibus and His Work*, traces "the rise, progress and decline of a theory of moral philosophy which prevailed in this country [England] for the greater part of the eighteenth century," a theory which held that we perceive that an act is right or wrong through a moral sense in much the same way that we perceive that an apple is sweet or sour through the sense of taste. Founded by Shaftesbury and developed by Hutcheson, it finally dissolved under the criticism of Kant. Shaftesbury's idea of the division of the self "into two parties," one judging the other, seems a foreshadowing of the Freudian Superego, but there is no mention in the book of Freud. Indeed, there is little to suggest that anything has happened in the world of thought since Hegel and his disciples.

A HISTORY OF PSYCHOLOGY IN AUTOBIOGRAPHY. Volume I.

By James M. Baldwin, Mary W. Calkins, Edouard Claparède, Raymond Dodge, Pierre Janet, Joseph Jastrow, F. Kiesow, William McDougall, Carl E. Seashore, C. Spearman, William Stern, Carl Stumpf, Howard C. Warren, Theodor Ziehen, H. Zwaardemaker.
Edited by Carl Murchison.

Clark University Press
\$5.00 6 x 9; xvii + 516 Worcester, Mass.

It is perhaps even truer in psychology than in other sciences that a knowledge of the history and personality of a worker aids one in understanding his work. It was therefore a happy thought of Professor Boring that led to this number of the *International University Series in Psychology*. Four volumes of autobiographies are planned, with additional volumes if

the idea proves fruitful. Among so many valuable accounts it is perhaps invidious to choose; we were, however, especially interested in those of Claparède and Seashore.



STAMMERING.

By *Elsie Fogerty*.

E. P. Dutton and Co., Inc.

95 cents 5 x 7 $\frac{1}{4}$; 64 New York

A brief discussion of the causes of stammering and methods of cure. The subject is one upon which we profess no competence; but the general impression we derive is that Miss Fogerty would probably be a good person to take charge of a stammering child.



THE MENTAL DEVELOPMENT OF THE CHILD. *A Summary of Modern Psychological Theory.*

By *Karl Bùbler*. *Harcourt, Brace and Co.*

\$3.00 5 $\frac{1}{2}$ x 8 $\frac{1}{2}$; xi + 170 New York

A brief account of the development of mental activity, interesting if not particularly startling. The description of the German child's acquisition of language indicates that our own ability in that language very closely approximates the average three-year-old.

The discussion of fairy tales we found interesting, but we missed any mention of the fact that children (at least some children) enjoy indefinite repetition of the same story; and they will insist on literal accuracy in the repetition.



SOCIAL PSYCHOLOGY. *The Psychology of Attraction and Repulsion.*

By *John J. Smith*. *Richard G. Badger*

\$2.00 5 x 7 $\frac{3}{8}$; xxv + 468 Boston

A dull collection of pious platitudes,

supported by weak reasoning and unproved and unprovable assertions. There is a complete lack of any searching thought. The book may, as the author hopes, be useful to "Y. W. or Y. M. C. A. groups;" but we doubt its value to genuine students.



BEHAVIORISM. *Revised Edition.*

By *John B. Watson*.

W. W. Norton and Co., Inc.

\$3.00 6 x 8 $\frac{3}{8}$; xi + 308 New York



DE OMNIBUS REBUS ET QUIBUSDEM ALIIS

FADS AND FALLACIES IN PRESENT-DAY EDUCATION

By *H. E. Buchholz*. *The Macmillan Co.*

\$1.50 (school edition) New York

\$2.00 (trade edition)

5 x 7 $\frac{1}{4}$; xiv + 200

The author of this delightful collection of essays is widely known, under the *nom de plume* of Ezekiel Cheever, as a trenchant and soundly realistic critic of current educational theories and practices. Several of the essays attracted much attention when they appeared in magazine form. Wit, humor, irony, and satire are effectively and entertainingly directed towards quackery, sham, and the uplift, as they nourish themselves in the field of education. We recommend the perusal of this book to everyone except school teachers and professors of pedagogy. They, poor things, would only have their feelings hurt, and we are opposed to cruelty to animals, even to those formerly designated at the University of Texas as "peedogs." The index is as entertaining as the rest of the book.

VIAGGI ED ESCURSIONI SCIEN-
TIFICHE DI LAZZARO SPALLAN-
ZANI.

By Giacomo Pighini.

L. Cappelli

Lire 40

Bologna

$7\frac{1}{4} \times 9\frac{3}{4}$; xvii + 441 (paper)

The experiments on digestion and the controversy with Needham on spontaneous generation, by which Spallanzani is chiefly remembered, were by no means the only activities of the versatile and energetic *Abbate*. In the intervals between researches on a variety of subjects, he made journeys in the Alps and Appenines, along the Italian coasts and to the Levant. These were primarily to enrich the natural history collections at Pavia, but Spallanzani also made the most of his opportunity for biological and geological observations. The account of these journeys, from his unpublished journals as well as from previously published books, is given in this interesting volume.



SIR ISAAC NEWTON. 1727-1927. *A Bicentenary Evaluation of His Work. A Series of Papers Prepared under the Auspices of The History of Science Society in Collaboration with The American Astronomical Society, The American Mathematical Society, The American Physical Society, The Mathematical Association of America and Various Other Organizations.*

The Williams and Wilkins Co.

\$5.00 $6\frac{1}{4} \times 9\frac{3}{8}$; ix + 351 Baltimore

This collection of essays was brought together at the initiative of the History of Science Society, collaborating with various other scientific societies, on the occasion of the bicentenary of Sir Isaac Newton. The several papers vary in quality

and importance as is, of course, inevitable in such a collection. The two which perhaps give the most novel light on Newton and his work are, first, that by George E. Roberts on "Newton in the Mint;" and, second, that by Frederick E. Brasch on "Newton's first critical disciple in the American Colonies—John Winthrop." Altogether the book is a valuable contribution to the literature of the history of science, and a credit to American scholarship. It is beautifully printed, but unfortunately lacks an index.



STUDIES IN THE LITERATURE OF
NATURAL SCIENCE.

By Julian M. Drachman.

The Macmillan Co.

\$4.00 $5\frac{3}{4} \times 8\frac{1}{2}$; xi + 487 New York

As its title implies, this book is not a history of natural science from the usual point of view but a study of natural science as literature. Charles Darwin is the central figure; Lyell and Uniformitarianism on the one hand, Erasmus Darwin, Lamarck and the rest of the early evolutionists on the other, lead up to him. Dr. Drachman has a talent for neat phrases, as in his felicitous description of Owen as "the tenacious but doomed champion of a retreating Old Guard, an academic army that dies mentally but never surrenders to a new truth." From his remark on Darwin's *Movements and Habits of Climbing Plants*: "Though there are a few tables of statistics on kinds of plants and their rates of growth, much of the book is written so that it can be read with ease and pleasure," we infer that he does not think much of statistics as a form of literature.

THE QUARTERLY REVIEW of BIOLOGY



THE BIOLOGICAL EFFECTS OF SHORT RADIATIONS

By CHARLES PACKARD

Columbia University, Institute of Cancer Research

I

FOR a generation, X-rays and radium radiations have been used in medicine and in biology for the purpose of injuring certain cells or tissues without permanently harming other parts of the organism. With their aid the radiotherapist may temporarily or even permanently check the unruly growth of neoplasms; the biologist may produce abnormal conditions in an organ or cell for the purpose of studying its normal functions. In both cases the end result rather than the process by which the result is obtained, has been the important matter under consideration. For this reason very little attention has been paid to the events which take place in cells from the moment that irradiation begins until the more obvious microscopic changes appear. But without doubt, information on this point is of highest importance; indeed, the little that we now know has thrown much light on many important radiological problems.

To find out what occurs in cells during and after irradiation it is first necessary to study the morphological changes. Much of this work has already been done; the histological effects are fairly well known,

and while there may be some disagreement in respect to details, the broad outlines of the degenerative processes are well recognized. This work is purely descriptive, in itself it gives little insight into the real nature of the changes or their cause. But a more careful examination of the finer details reveals reactions which have previously been overlooked. These are concerned with the changes in the chemical constituents of protoplasm. And at this point the biologist must rely on the chemist for a correct interpretation of the phenomena. To be sure, analysis has thus far proved so difficult that little is known about the various transformations which occur in the proteins, fats, and carbohydrates as a result of irradiation, but undoubtedly the much needed facts will gradually be obtained. Finally, the changes which can be observed, whose chemical nature is beginning to be known, are produced by the transformation of radiant energy in the cell. In order to picture the mechanism by which these changes are brought about we must rely on physical facts and assumptions. Indeed, a successful biological experiment with these radiations must be made with the help of a physicist who can arrange prop-

erly the conditions of exposure and make the essential measurements. These three sciences, then, must contribute to the solution of the problem of what takes place in a cell as the result of irradiation.

X-rays and radium radiations are especially valuable in biological research because of their ability to penetrate deeply into cells in which they may affect some particular region without causing irreparable damage to the rest. This differential action is not due to any selective power of the rays; they do not give up their energy and thus produce an effect in the sensitive regions only, while passing through the resistant portions without stopping. All parts of the cell and all kinds of cells have about the same power of absorption; whether they are injured or not depends on their physiological condition at the time of exposure and afterward. But the factors which are responsible for this condition are thus far practically unknown.

Sensitivity to radiations is sometimes spoken of as though it were a peculiar phenomenon, different from general sensitivity. This is quite incorrect; cells that are susceptible to X-rays and to radium are also susceptible to other stimuli. During mitosis they are more easily injured by agents of very different kinds than they are at any other moment. But these radiations differ from heat, cold, and chemical action in that they can bring to light small differences in susceptibility not readily shown by other means. And they do this with the expenditure of an exceedingly small amount of energy which is absorbed by only an infinitesimal proportion of the atoms in the irradiated material. But the effect of such absorption is great. As much energy as will warm a cup of cold water would, if absorbed in the form of penetrating radiations, kill a man. In this respect their

action is analogous to that of an active poison, such as ricin, which even in very minute quantities is fatal.

Nor have the radiations any power to produce effects of a novel kind; the degenerative changes which follow an exposure to X-rays or to radium are not new to pathologists. Heat, cold, the electric current, and many chemicals bring about the same type of injuries. This does not mean that the mode of action on protoplasm is the same; in all probability it differs greatly, but the end result is alike in all cases.

The lively interest in the effects which these short radiations produce on living cells and organisms may be realized from the fact that an abstract journal which reviews only investigations on these topics, together with those on ultraviolet and visible light, cites upwards of 5000 titles each year. Of these more than half deal directly with medical problems of diagnosis and treatment, but a large proportion of the remainder has to do with the morphological, physiological, and chemical changes produced in protoplasm by penetrating radiations.

In this review I shall discuss some of the topics which are engaging the attention of radiologists at the present time, omitting all reference to the very extensive literature on the action of ultraviolet rays, the visible spectrum, and of mitogenic rays. And I shall emphasize the results which throw light on the reaction of the cell rather than those which are concerned with the entire organism. For the behavior of the organism after irradiation is a result of the direct action of the rays plus many secondary responses which greatly complicate the total effect. It is obviously impossible to treat the subject in detail, or to cite more than a fraction of the literature which has been accumulating for more than thirty years. Nor

can I discuss the results of those experiments in the field of embryology and genetics in which the interesting feature is the response of the organism rather than the means by which the results are obtained. The older literature also is referred to only occasionally, for it has been fully reviewed elsewhere (18, 63, 95, 110).

II

MORPHOLOGICAL AND PHYSIOLOGICAL EFFECTS

When a cell is exposed to X-rays or to radium radiations it quickly begins to show morphological and physiological changes, some of which can easily be seen, while others can be demonstrated only under favorable conditions. If we examine a cell during exposure, when it is still alive, we observe a series of events which lead to evident injury, a condition from which it may or may not recover, but we miss many details because they are invisible. By proper staining methods these can be brought out, but in the process others are lost to view. Both means of study are essential to a clear understanding of the effects produced by radiations.

The recent work of Nadson (70) on living yeast cells gives for the first time a clear picture of the progressive changes which begin almost as soon as the exposure commences and terminate in the death of the cell. His ingenious methods for radiating an individual cell warrant description. He fastens the radium salt, enclosed in an ebonite capsule from which the beta rays can escape, to an object lens. This is attached to the nosepiece of the microscope. Then with another lens he examines the field and selects some cell for study. Next he turns the nosepiece so that the radium is in position a few millimeters above the yeast. At the end of exposure he can examine the particular

cell which he had previously selected, a necessary procedure in view of the wide variation in the response of different individuals even in the same pure culture.

The first visible effect consists in an increase in the number of fat droplets, which are normal constituents of the yeast cell. This change in the physical and perhaps chemical condition of the fats is not injurious if irradiation is not prolonged; such cells may grow and divide (36). Next, the protoplasm becomes turbid, due to the appearance of granules which are undoubtedly protein in nature. What has happened is that the colloidal protein has undergone a partial denaturing, that is, it has become insoluble. These changes are at first reversible, for the turbidity may disappear, in which case the cell recovers. Bordier (10) first described this phenomenon in proteins irradiated *in vitro*, and it has been demonstrated by others. Rajewsky (85), who studied the effect of ultra-violet rays on pure pseudoglobulin solutions, describes the appearance of the granules, which in his material were smaller than those which can be seen in yeast, and shows that they increase in number to a maximum, then nearly disappear, then reappear in smaller numbers, this rhythm being repeated several times within the course of a few hours. He compares this with the course of the erythema reaction in which there is a similar rhythm. With longer exposures the fat droplets do not seem to increase further but the number of protein particles does. The permeability of the cell membrane at first decreases, as shown by the Neutral Red test; while after long exposures it increases, and is accompanied by a coagulation of the protoplasm.

This investigation by Nadson constitutes an important contribution to our knowledge of radiation effects, for it

gives an insight into the first reactions of the living cell, a subject which has long been neglected.

In addition to these changes there may be seen in other kinds of cells an extensive vacuolization of the protoplasm (6) and a breaking up of the filamentous mitochondria into granules, a reversible reaction, since later they may resume their normal appearance. These changes can be seen more clearly in stained material in which, after severe irradiation, the mitochondria are found to be much altered in shape and in their arrangement in the cell. Probably some disappear entirely (109).

There is very little difference between these changes which follow irradiation and those which accompany degeneration induced by other means. The Lewises (61) find that when normal tissue culture cells are deprived of embryonic extract they eventually pass through a series of changes closely parallel to those which have just been described. First there is an accumulation of small granules in the cytoplasm which grow in size and number and take the Neutral Red stain. The mitochondria fragment and disappear in part. Before actual death occurs several irreversible changes can be seen. One is the disappearance of the degeneration granules and the growth of others which do not stain in Neutral Red.

It is not surprising that this sequence of events is the same in both cases. Protoplasm appears to react to all kinds of adverse conditions in the same way. That the histological changes are the same has already been mentioned. The observations just cited show that this principle holds true even in respect to the finer details of the degeneration process. Further study may reveal some of the changes which precede these and allow us to determine their nature more precisely.

In the living cell after irradiation the

nucleus appears to be unchanged at first, even though the protoplasm gives clear evidence of being injured (51); but stained material shows that it is really profoundly modified. Such changes can be seen best when the cell is in mitosis. At such a time the chromosomes are found to be fragmented, or stuck together, or misshapen. At the metaphase some may fail to divide completely, the halves remaining attached by long chromatin bridges. After division the nuclei are often pyknotic. The asters and spindles are not affected unless the whole cell is severely injured, in which case they may fail to develop properly.

Although we can detect changes in one part of the cell before some other portion is altered, this is not proof that the one is more severely damaged than the other, nor can we judge the extent of the injury by the appearance of the cell at any particular moment. One that is to all appearances moribund may recover, while another that looks normal after exposure may die later.

When short, penetrating radiations are absorbed in a cell they quickly change the rhythm of mitosis. Even a brief exposure to gamma rays prevents those cells which were about to divide from beginning that process (14). Unless the irradiation is long continued or very intense they suffer no visible injury; indeed, they begin to divide soon after the exposure stops, giving no evidence that they have been permanently harmed. In tissue culture experiments, in which these phenomena can be seen to advantage, this temporary check in the onset of mitosis is followed by a very considerable increase in the number of dividing cells, the result being that the total number of divisions occurring within the space of a few hours after exposure is about normal (15). I have observed this in radiating *Paramoecium*, a

temporary fall in the division rate being often followed by an increase to a point well above that of the control. But the total number of divisions at the end of a few days is the same in both.

Cells which are already in mitosis when irradiation begins, complete the division on which they have entered; they are not checked (105). This is true even when the dose is so severe that it leads eventually to death (83). Richards (90) has found that *Planorbis* eggs, exposed during mitosis, are very materially accelerated for a brief time; and I have seen this also in the eggs of *Arbacia* (72). The result of this response is that immediately after exposure one may find in an actively growing tissue a large number of mitotic figures. But a little later none can be seen (88). This quiescent period lasts for a varying length of time, depending on the dosage, and is followed by a return of mitotic activity. Such divisions however are usually abnormal, but it is a curious fact that in a tissue which has been severely injured one may find perfectly normal division figures lying among many that are very aberrant. This I have seen many times in irradiated *Drosophila* eggs.

The absorption of radiant energy by the cell is followed by a number of reactions which undoubtedly have their origin in physical and chemical changes in the protoplasm. One of these is the alteration in the rate of protoplasmic streaming. In plant cells Williams (116, 117) finds that both X-rays and gamma rays increase the rate of flow at first, while longer exposures have the reverse effect. Zuelzer and Philipp (124), who describe an acceleration in streaming in many types of Protozoa, suggest that this is a result of a lowering of the viscosity.

Changes in viscosity are important signs of deep lying physiological changes which

occur in cells in both normal and abnormal environments. For this reason a very considerable amount of work has been done to determine how the short radiations may affect the consistency of protoplasm. The results thus far have been conflicting. Fairbrother (30) observed a marked decrease after irradiation, amounting to 40 per cent of the original value; while Wels (113), who exposed serum and globulin solutions *in vitro*, found an increase. Weber (112) could see no change at all but felt that there may have been some. That the age or sensitivity of the cell may determine which reaction is to occur is suggested by Jannson (51), who finds that in adult leucocytes the protoplasm is liquified, while in immature myelocytes, which are more sensitive, it is coagulated. Finally, Nadson (70) shows that the viscosity may decrease at first and later increase. A theory which harmonizes these discordant results is offered by Lepeschkin (60). Changes in viscosity, he says, are produced by different agents which bring about a gradual decomposition of the principal compounds of protoplasm. When such decomposition occurs, the products "join in the dispersed phase of protoplasm and increase its viscosity. At the same time the removing of the lipoids from the dispersion medium may increase the disperse phase or decrease the viscosity of protoplasm. Both opposite changes of the viscosity may be produced by any injury effected, but its distinct decrease could evidently be observed only if the decomposition is not marked enough, while in the opposite case an increase of viscosity occurs."

It is probable that the permeability of the cell membrane is increased by both X-rays and gamma radiations, although several investigators have been unable to demonstrate it. Richards, for example, (91) exposed several kinds of marine eggs

and larvae to X-rays but found no evidence of an increase; and more recently Kovacs (58) has stated that toward serum albumen the cell membrane shows no increase after irradiation. On the other hand he demonstrates that the simpler proteins, dyes, and some other substances diffuse out more rapidly after exposure than before. This suggests that the effect is chiefly on the membrane itself. Kovacs believes that the result is due to the change in the electric charge of the ions at the surface. I have found (72) that the rate of penetration of ammonia into *Paramoecium* is noticeably quickened, especially by the slow beta rays, which are more likely to be absorbed at the membrane than are the more penetrating rays. The evidence, however, is not sufficient to warrant the statement that this region only is affected. More probably the change in permeability is a symptom of some general physiological change in which the entire cell is involved.

Whether short radiations act upon the lipoids of the cell is a much debated question. Some years ago Schwarz (98) declared that lecithin is changed to trimethylamin and that this substance is responsible for the injuries which develop after exposure. But this is very doubtful; sperm cells, which contain very little lecithin, are sensitive. Later Werner (115) stated that cholin is formed by the action of radiations on lipoids, and has a cytolytic effect. Neither of these views has been confirmed. But Nadson's observations show that the fats are in some way altered, a fact which assumes importance when we consider their rôle in the permeability of the cell membrane. What the precise relation may be between permeability and the radiated lipid substances is still to seek.

Many divergent opinions are held regarding the effect of radiations on the

hydrogen ion concentration of protoplasm. When irradiation is severe and the cells are injured, the pH turns to the acid side, as would be expected. Many proteins, irradiated *in vitro*, respond in the same way, but this is by no means a general rule. Karczag (54) believes that in the living cell the acidity tends to rise but that such a change cannot always be demonstrated because protoplasm has great powers of regulation, retaining its normal pH until it is severely injured.

That cells may recover from injuries produced by the radiations can easily be demonstrated, especially in the Protozoa, which are extremely resistant. Crowther (21) had to give *Colpidium* the huge dose of 80,000 Roentgen units in less than twenty minutes if he wished to kill the cells. If a smaller dose were given, or the same dose in a longer time, the cells gave every appearance of being moribund, but they recovered perfectly within a few hours and could be irradiated repeatedly on successive days without showing any permanent injury. *Drosophila* eggs also, though relatively sensitive (180 units kill half of a population of newly laid eggs) must be given a fairly intense dose within a limited time if they are all to be killed. Should the dose be light only a few eggs, that is, the most sensitive, will die, the others continuing to live even though the total dose is sufficient, if applied in a short time, to kill every one (75).

The environment of cells after irradiation is an important factor in determining whether they will or will not recover. Wood and Prime (123) found that tumor cells irradiated *in vitro* and inoculated at once into healthy animals, failed to grow; but if instead, they were put into plasma, they lived and multiplied.

There appears to be also a correlation between the rate of division after ex-

posure and the ability to recover. If *Drosophila* eggs are irradiated at ordinary temperatures and then divided into two portions, one of which is kept at 28° C. and the other at 17°, the latter will survive in a much larger proportion than the former (80). A similar result was reported by Strangeways and Fell (104), who worked with chick tissue cultures. The reason for the difference in behavior of the two lots was due, they think, to the lessened metabolism in the eggs kept in the cold. Whatever may be the explanation, the fact is clear that reparative processes go on more readily when cell division is checked.

What actually happens in the regeneration process is unknown. Evidently the initial changes in the protoplasm are reversible. The question is important, for the value of radiations in therapy and in biological experiments depends on the ability of some cells to recover from injury while others are destroyed.

III

THE LATENT PERIOD

The first changes which take place in an irradiated cell are so slight that they are invisible except under very favorable conditions. Only in fairly transparent, living cells which may be examined under high magnifications can the alteration in the physical state of the proteins and fats be detected; the acceleration or retard in the rate of cell division can be demonstrated only in tissue culture preparations or in dividing eggs. And unless the irradiation is intense or prolonged, the cells recover, giving no evidence of injury.

But even though cells eventually die in consequence of a severe irradiation, the first easily observed signs of injury make their appearance only after an appreciable time, developing gradually in a way analogous to the development of a photo-

graphic plate. This interval is called the Latent Period, a term used particularly by those who judge the effect of the rays by macroscopic signs. For example, the period for the human skin varies from a few days to two weeks, this being the interval between exposure and the first appearance of redness. The term is a convenient one, even though in one sense no latent period exists. What occurs between the time that the cell constituents begin to change under the influence of radiations and the time when the tissue shows very obvious injury is not known in any detail; but evidently the degeneration processes continue long after irradiation ceases.

The length of the latent period depends on a number of factors, of which one is the division rate of the cells. In the testis, for example, where this rate is high, the spermatogonia begin to show cytolytic degeneration about two hours after exposure (96), while injuries to the cutis may be many days in developing. To explain this condition Heinecke (41) suggested that the latent period ends when the irradiated cells die a natural death. That is, radiations affect only their reproductive capacity, the nutritive being unimpaired. If then a cell normally has a short life the visible effects on the tissue to which it belongs will quickly appear. The objection to this hypothesis is that some irradiated cells, especially eggs, begin to show injuries after many cell generations, as Hertwig and others have shown.

Another factor which determines the length of this period is the intensity of the dose. When great, the time elapsing before an extensive injury appears is short, and vice versa. Prime (82) exposed chick embryo heart tissue to the gamma rays from 100 mg. of radium and then planted it in serum. After a two-hour dose the cells pulsated and divided, but ceased by

the end of the second transfer. After a thirty-minute dose their activities ceased only at the time of the fifth subculture.

Oftentimes an irradiated organism will continue in an apparently normal condition until it undergoes some large morphological or physiological change, such as gastrulation, hatching from the egg, or metamorphosis. Thus Vintemberger (107) exposed one of the blastomeres of the frog embryo in the two cell stage, protecting the other by a lead screen. After a rather heavy dose of X-rays the embryo developed normally until the time of gastrulation when the irradiated half ceased from further growth while the remainder continued. When a small dose was applied, development was normal but retarded. So also, irradiated *Drosophila* larvae may continue to grow until the time of pupation or the emergence of the imago.

The reasons for the gradual development of injury are not clear. Of the theories advanced to explain the phenomenon many are based on the reactions of large organisms, in which the secondary effects of irradiation occupy a large part in the clinical picture. Others based on the reactions of cells seem to come closer to being working hypotheses. Schwarz (99) suggests that the degeneration of proteins is the essential factor. In such a change, these become what he calls "actino-proteins," which are poisonous, although the toxic effect is not great. Later, by further transformations they become more and more toxic and their action on protoplasm produces degeneration products which are inflammatory. The basis of this hypothesis is the well known fact that after irradiation there may be a slight response, often an acceleration, which is followed by apparent recovery and then by more extensive injury. This is characteristic of the erythema reaction; it can

also be demonstrated in dividing eggs. The first response is due to the actino-proteins directly; the second, to the derived products which are gradually formed and hence exert their effect some time after exposure. These products are called "necrohormones" by Caspari (16). When they have killed the cells which produce them they are supposed to escape into the body and to bring about a general reaction.

Flaskamp (32) introduces another idea. The degeneration products, whose nature he does not discuss, stimulate the production of antitoxins. If the dose is weak, these are sufficient to overcome the toxic effects, and no damage results. But if the dose is strong they are not adequate, and injury appears. The latent period is the time during which these two antagonistic forces are at war and before the toxic substances have gained the victory. One merit of this hypothesis is that it takes into account the tendency of a cell to recover from injury. This is a general biological phenomenon which is usually neglected by those who form theories to fit particular cases. But if Flaskamp's idea is true we must believe that antitoxins are less effective, or produced in smaller quantities during the anaphase of mitosis than during the resting period.

These are little more than formal explanations of the problem; the agents which produce the end results are really unknown. Some observations by Knipping and Kowitz (56) indicate that after irradiation of an entire organism the proportion of globulins in the serum is increased, while that of albumen is decreased. The clinical effect of the treatment resembles that which follows the injection of foreign proteins. This does not prove, however, that the two phenomena are related.

IV

SENSITIVITY

That different kinds of cells and tissues vary in sensitivity was observed very soon after the discovery of X-rays in 1895. The first workers, who naturally did not realize the danger connected with their experiments, found that the skin is susceptible, a moderate exposure producing a slight burn or erythema which appears some days later. This skin reaction soon became a measure of dosage, and it is still widely used although by no means satisfactory. The output of the first tubes was highly variable and the early investigators determined the intensity of the beam by observing the shadow cast by the bones of their hands on a screen. While these brief exposures produced no burns, their cumulative effect was very serious, many workers losing their lives years later as a result. Among these martyrs to science was Bergonie, who before his death in 1925 made contributions of greatest value to radiology.

Further studies make possible the arrangement of the different mammalian tissues in the order of their sensitiveness. In such a list (92) the germinal epithelium and blood forming organs stand at the top, while at the bottom, being least susceptible, are the liver, and nerve and fat tissue. A fixed order is not possible, for some tissues, such as the skin, vary in sensitiveness with the age of the individual, being highly susceptible in young children and comparatively resistant in the aged. Health and disease are also controlling factors in determining the reaction to radiations.

There is a striking difference in sensitivity between different types of cells in the same organ. The most familiar example is the testis, in which the sperms, in their stages of development, show

marked variations in response. The first spermatocytes are usually regarded as more susceptible than the spermatogonia or the fully formed sperms. So also, the lining of the blood vessels is more easily injured by radiations than the surrounding muscular coats.

During the division cycle, cells show marked variations in sensitivity. A dose applied during the resting stage may produce no visible injury, but if given during actual mitosis, may be lethal. And the effect is much greater at some stages of division than at others, although just what stage is most sensitive has not been agreed upon. Strangeways and Hopwood (105) observed that cells already in division continue to divide if irradiated not too severely, while those that are ready to start the process are inhibited for the time being. From this they conclude that just before the prophase the cell is more sensitive than at any other time. Mottram's early experiments (67) indicated that the metaphase is the moment of least resistance, and this view has found wide acceptance. Regaud (87) finds that during the prophase and anaphase sensitivity is at its height, while Vintemberger (106) in a recent publication states that the telophase is the critical time. He exposed frog eggs to brief but intense radiation during the periods which experience had shown were occupied by the various division stages. After exposure the eggs are allowed to develop, the criterion of effect being the percentage of embryos dying. He found that susceptibility rises from the prophase to the telophase and then falls abruptly when division is completed.

In view of Richards' observation (9) that dividing eggs, when exposed, break quickly through the mitosis which progress, it is difficult to say how single stage may continue. If it

mally very short, as is, for example, the metaphase, the actual time the cell can be exposed in such a stage may be so short that ordinary irradiation may not affect it at all. The question of the most susceptible stage in mitosis can best be settled by observations on living cells in which the changes following irradiation can be watched in the order of their appearance.

Even more debated is the question of the most susceptible part of the cell, a problem rendered difficult because of the different criteria by which the effect of radiations is estimated. That the nucleus is highly sensitive has been demonstrated in many ways. The long series of experiments by Hertwig and his students (42, 43) showed that the beta and gamma rays of radium can injure the sperm or egg nucleus without destroying either cell's activity in the fertilization process. An irradiated sperm is motile and can initiate development in a normal egg. If it has been slightly irradiated it interferes with mitosis, the eggs soon dying. But if it is severely injured it plays no part in subsequent development, which is fairly normal. The nuclei in the growing embryo are haploid. Here then is a seeming paradox in that a slightly injured sperm causes more disturbance in development than a severely injured sperm.

Dalcq (24) has recently repeated these experiments on the frog egg, using X-rays, radium, and ultraviolet light. When the sperm are exposed to the latter and then added to normal eggs the paradoxical effect is very evident; when X-rays or radium are employed it appears only occasionally.

In the irradiated egg of *Chaetopterus* (73) the nucleus may be so injured that it can take no part in the first cleavage division after a normal sperm has entered. The protoplasm of such an egg is not, how-

ever, permanently injured. The egg membrane lifts off, and the sperm is drawn in just as in normal eggs. The normal nucleus plays no part in the development which ensues, cleavage taking place under the influence of the sperm nucleus alone. Another experiment (108), mentioned because of the ingenious method used, again demonstrates the susceptibility of the nucleus. Frog eggs are irradiated through small holes in a lead plate, the holes being so spaced that the rays passing through them strike the nuclei of the blastomeres in the two cell stage. Eggs thus treated die, but are seemingly uninjured if the narrow pencils of rays are allowed to strike only the protoplasm. No further proof is needed to show that chromatin is a highly susceptible part of the cell.

More delicate effects of radiations on the nucleus have recently received much attention. When *Drosophila* is irradiated the nuclear mechanism may be so altered that the rate of crossing over during the synaptic period is modified (65). The work of Muller (68, 69) and others shows in addition that out of the entire chromosome complex a single gene may be modified, the change being demonstrated by genetic tests. Cytological proof of visible malformations in the chromosomes is furnished by Dobzhansky (28), who shows that irradiation may result in the breaking of one or more of the chromosomes into fragments of varying proportions. Of great interest is the fact that the actual size of the fragments is roughly proportional to their size as determined genetically. Radiations have proved a useful means of inducing a rapid mutation rate and of disarranging the mechanism of heredity. The genetic results of such experiments are of greatest interest, but since they lie beyond the scope of this review, they can only be mentioned.

From this evidence one might conclude that radiations produce injuries in the chromatin alone. This is not necessarily true. The cell is a unit, and whatever affects one part must affect the rest also. But it may be that the cytoplasm has a greater regulative power than the nucleus and hence can recover from an injury. Needless to say, any cell or any part of the cell, no matter how resistant, may be destroyed by radiations if the dose is strong enough.

In general, rapidly growing tissues are highly susceptible. So also are cells in which differentiation is not great. For example, the undifferentiated formative cells of *Planaria* can be practically destroyed by radiations although the animal itself continues to live for some time (22). The developing eggs of *Drosophila* are easily killed by small doses of X-rays; the larvae are more resistant; the pupae, still more so, while the adults succumb only to very large doses (66). Bergonie and Tribondeau (4) summarized their conclusions regarding the reaction of cells to radiations in the statement that sensitivity varies directly with the reproductive capacity of the cell and inversely with its degree of differentiation. This principle is true in general, although there are many exceptions. A rapidly growing melanoma is highly resistant, while an inactive basal cell sarcoma on a similar site is very responsive.

When we seek a reason for these differences in sensitivity among different kinds of cells, and in the same cell at different periods of its division cycle, we are faced with two difficulties neither of which can be overcome at present. One is that we know little of the nature of the changes which radiations produce, and the other, that we are still ignorant of the nature of the normal functions of the cell which the radiations disturb. It is not surprising

therefore that we cannot form any general hypothesis which will explain all of the various results which have been obtained.

The suggestion has often been put forward that sensitivity is dependent on the metabolic rate of the radiated cells. Dormant seeds, in which respiration is at a low ebb, are resistant, but when they germinate, their susceptibility rises with the rate of respiration (57). The rate of oxygen consumption in normal and pathological tissues is said to vary directly with their sensitivity (35). Instances of this kind could be multiplied. But there are important exceptions. For example, the metabolically active cells of the liver are highly resistant; and the eggs of *Ascaris*, radiated under anaerobic conditions when their metabolism is much reduced, are only a little less sensitive than when they are radiated in air (45). Furthermore, there is no apparent relation between the variations in susceptibility during mitosis and the metabolic rate. The experiments of Rogers and Cole (93) show that during cleavage, heat production is constant; and Shearer (101) found that the rate of oxygen consumption and CO_2 production is steady, not showing fluctuations during the stages of mitosis. These instances, however, are not sufficient to outweigh the large amount of evidence which indicates that there is some connection between susceptibility and the metabolic rate, or some physiological condition closely bound up with it.

Another hypothesis to account for sensitivity to radiations is based on the degree of hydration of the protoplasm. Schaudinn, in 1899 (94) first pointed out the fact that those Protozoa whose protoplasm is most fluid are also most susceptible. Petry (81) also has shown that seeds are more sensitive when swollen with water, while they become resistant if allowed to dry a little. In this connec-

tion it should be recalled that in young and active cells, such as are found in growing root tips of plants, the protoplasm is much more fluid than it is in adult cells. During cell division the viscosity of protoplasm undergoes striking changes, rising abruptly during the prophase, falling sharply at the metaphase and then rising again gradually (40). The precise relation between the various stages of mitosis and protoplasmic viscosity is not wholly clear, but the phenomena are of interest because they appear to run more or less parallel with the changes in susceptibility to radiations, and they are the only phenomena thus far known which show this relation. According to Heilbrunn (40) "the periodic cycle of rhythmic changes in viscosity of dividing cells is almost certainly related to the rhythmic changes in susceptibility of dividing cells to various toxic substances."

Some attempts have been made to correlate the degree of sensitiveness with the amount of radiant energy which the cell absorbs. The higher sensitivity of the nucleus was explained by the fact that in this cell organ there is a higher concentration of phosphorus which, because of its atomic weight absorbs more energy than carbon, oxygen, or hydrogen. But actually no such correlation exists. Red blood cells with their high iron content are less sensitive than the lymphocytes, which contain very little iron. And experiments show that the amount of radiant energy absorbed by blood, muscle, fat, Locke's solution, and pure water, are practically identical. That is, the differences, if they exist, are too small to be measured with the apparatus at our command. We must believe therefore that the same amount of energy is absorbed by all kinds of cells. The different quantitative effects may be due to the chemical make up of the cells, or to the relative

stability of the compounds, or to differences in regenerative power. But these are only guesses; there are at present few data on which they are based.

The question of sensitivity is the chief problem before the radiologist, for all work with radiations depends on the fact that in the tissues or cells under exposure some part will respond more quickly than another. This is the basis of radiotherapy and of those genetic experiments in which the chromatin or even some minute portion of it is altered while the remainder of the organism is not permanently changed. The problem is still unsolved. As Holthusen remarks, "The radiosensitivity of cells is closely bound up with their chemical structure and with their organisation, yet we do not know what those substances are which are responsible for the great differences in susceptibility." (48).

V

STIMULATION

A question which has been much debated by students of radiology is whether cell activities can be promoted by very light doses of radiations. The belief that this may be possible is based on the Arndt-Schulz law, which states that many agents, when applied in small doses, bring about an acceleration; in medium doses, a depression, and in large doses, a complete stopping of vital actions. This principle was for a time widely accepted by radiotherapists, who explained the occasional rapid growth of tumors after radiation by saying that the dose had been too weak. Such an explanation is hardly logical, for the law is of limited application; indeed, it is not a law at all, but only a generalization whose value is doubtful.

Those who have found evidence of acceleration have used the word "stimula-

tion" to describe the phenomenon. The term is unfortunate, for in its proper sense it means any change in the state of the organism, whether excitation or depression. But the latter meaning has been disregarded; stimulation in radiological literature refers to an acceleration in the rate of growth or to an increase in functional activity. Usually it implies a reaction favorable to the organism, although sometimes it is used to refer to any quickening in the normal tempo of vital activities, even though the end result is an obvious injury. I shall use it in the former sense in this discussion.

A large amount of the experimental work carried on to determine whether or not radiations can promote growth has been done on plants, especially young seedlings. Many investigators find that the rate of growth of the roots or shoots is accelerated by weak doses, or that the radiated plants have stronger stems and heavier leaves than the controls (52, 38, 50). Their conclusions, however, are open to criticism because they are based on measurements of very few individuals; the factor of normal variability is practically neglected. Jüngling, for example, believes that half a dozen seeds are sufficient for a single test, with one or two for controls. Those who have repeated these experiments using very large numbers of specimens are outspoken in their belief that no stimulation occurs (100, 2). Not uncommonly a group of lightly radiated seeds may be found to grow faster than the controls, but such isolated cases are not significant. On the other hand, Arntzen and Krebs (3), whose technique was excellent, found a slight but real acceleration in the growth of peas during the first two days after irradiation. This was followed by a retardation in every case.

When the shoots of various plants are

lightly irradiated in the proper stage of development their buds open sooner than do those of the controls. Weber (111) suggests that the acceleration may be due to a change in permeability or to increased oxidation. Reiss (89), however, believes that there is no evidence of real stimulation, that is, of quickened normal growth, for he finds no increase in the number of mitoses in the irradiated material. On the contrary, the cells are clearly injured as shown by the shrunken protoplasm and the peripheral position of the nuclei. Furthermore, they are decidedly larger than those of the control plants. Such an increase is common in irradiated cells. Nadson (70) believes that it is due to increased cell turgor. It cannot be regarded as an evidence of healthy growth but rather of injury. The most enthusiastic believer in the stimulating action of radiations is Stoklasa (103), who states that "in weak concentrations, emanation affects favorably mitosis, plant development in general, the interchange of gases, the activity of chlorophyll, and of flowering and reproduction." Some doubt is thrown on his statements by the fact that the doses which he found large enough to produce a retardation were much smaller than those which Falta and Schwarz (31) report as stimulating. The results have not been confirmed.

Many experiments show that weak radiations may accelerate the rate of mitosis and of growth in animal cells. In most cases this reaction is short lived, or terminates in an obvious injury. Among the first to describe the quickening effect were Lazarus-Barlow and Beckton (59), who treated *Ascaris* eggs with very minute quantities of radium. Those eggs that were exposed for long periods at low temperatures were found to be in the two-cell stage while the controls were still uncleft. From this they conclude that under the

influence of these radiations "cellular division proceeds at an accelerated rate." The observations did not extend beyond the two-cell stage. I have observed also that the first division of *Arbacia* eggs may be slightly accelerated, but the effect seems to disappear very soon (72). Richards (90) reports the same results on *Planorbis*. Obvious injury, however, appeared during later development. Hoffmann (44) found that when frog eggs are lightly irradiated they often develop more rapidly than the controls. He is careful to state that stimulation can be demonstrated only if one is lucky; that is, the internal and external conditions of the eggs must favor quickened growth.

The experiments of Markowits (64) on *Paramecium* are widely cited as giving evidence of stimulation. But his methods were such as to throw some doubt on the value of his conclusions. He made no daily isolations of the descendants of the irradiated cells, nor did he determine the division rate, but only counted the number of individuals alive on the tenth day after exposure. His data show that the irradiated cell, in one test, had divided ten times while the control had divided but seven times. This low score for the control indicates that the culture medium was faulty.

There are some experiments which show that the rate of cell division may be definitely accelerated and that this condition may continue for some time. Of these the most striking are those of Nasset and Kofoed (71), who exposed mass cultures of *Endamoeba dysenteriae* to radium. In one test in which the exposure continued for eight days, the number of cells at the end of the third day of irradiation was about five times as great as in the controls. Four days after the removal of the plaque there was a great reduction in the population. The cells showed characteristic

injuries,—abnormally large size, vacuolization of the protoplasm, atypical nuclei and mitoses. Cells which were not severely injured apparently recovered, for the irradiated cultures could be kept alive by transplantation.

In a few instances true stimulation seems to occur; that is, the quickened tempo of growth is not followed by any observable abnormality. Hastings, Beckton, and Wedd (39) exposed silk worms in various stages of development. When eggs are treated they hatch out earlier than do the controls; if the larvae are irradiated the cocoons are heavier than normal. In these experiments the number of individuals treated was adequate and the tests were repeated in successive years. Similar results are reported by Blumenthal and Williams (8), who used grasshopper eggs, treating them with X-rays and with radium. But these observations, standing alone among the large amount of negative evidence, are not sufficient to warrant the conclusion that true stimulation of growth follows exposure to weak doses of radiations.

The same statement may be made in regard to the experiments on the effect of the radiations on cell functions. Stephan (102) draws a sharp distinction between growth stimulus, which he denies, and functional stimulus, which, he believes, can be demonstrated. He finds that the activities of the kidney, spleen, and thyroid are augmented after mild doses. But Czepa (23) in a careful review of the entire question of stimulation shows that the functional increase, which is an undoubted fact, follows in every instance a destruction of the more susceptible cells in the radiated region. It is therefore a response to the action of degenerating cell products rather than a direct stimulation by the rays.

Some work has been done on the effect

of radiations on the respiratory rate. In many cases this appears to be increased, but whether this result is normal or pathological is not certain. Blumenthal and Williams (8) have made quantitative measurements on the rate of oxygen consumption in radiated grasshopper eggs and find a definite acceleration. The higher rate becomes noticeable five days after exposure. This is a very long latent period, considering the fact that the eggs were dividing rapidly. Kimura (55), who studied the CO_2 output of radiated tumor cells, exposed *in vitro*, found an increase which was not always associated with the rate of mitosis. That there may be no relation between the rate of CO_2 production and growth is the conclusion of Redfield and Bright (86). Their irradiated seeds, from which CO_2 was given off more rapidly than from the controls, were obviously injured, some not germinating at all. On the other hand, Bersa (5) reports a decreased respiratory rate in irradiated beans, while Wels (114) is unable to demonstrate any change whatever in muscle cells, in yeast or in bacteria.

The many experiments in which entire animals are exposed to radiations show that the respiratory rate is lowered. Such results are difficult to interpret, for when all of the organs of a large animal are irradiated each responds in its own way, depending on its sensitivity at the moment. The CO_2 output is thus an average of the activities of many parts. While this is of clinical interest, it does not throw light on the action of the rays on single cells.

The evidence now at hand points to the conclusion that radiations do not directly stimulate normal activities of the cell; their primary effect is always an injury from which the cell may recover perfectly. But the degeneration products which arise after irradiation may temporarily quicken the tempo of some normal processes, such

as protoplasmic streaming and mitosis; an acceleration which is followed by a retardation and often by very obvious injury. Such reaction is secondary, and is not true stimulation in the sense in which the term is used in radiological literature.

VI

PHYSICAL THEORIES OF THE ACTION OF RADIATIONS

A theory to explain the way in which radiant energy produces changes in a living cell must be based on certain physical assumptions regarding the nature of this energy and of the atoms and molecules which it affects. In the discussion which follows I have included only those assumptions on which the biological theories are based, and have purposely omitted all other matter.

There are two ways in which we may picture a beam of radiant energy, whether it be of visible or ultraviolet light, X-rays or gamma rays of radium. We may regard it as consisting of electro-magnetic vibrations, or we may picture it as made up of discrete bundles of energy or quanta, which are shot like bullets from their source. Both conceptions seem to be necessary at present, for there are many phenomena which can most readily be explained by one or the other but not by both. The first prevails when we describe the quality of the beam in terms of wave length. Short rays, like the gamma rays of radium or those produced by an X-ray tube running at high voltages, have waves ranging from 0.01 to 0.1 Angstrom units in length. (This unit is 1×10^{-8} cm.) Soft rays produced by special tubes at potentials of 10 KV. or less are relatively long, that is, more than 1.5 Angstrom units. They are thus more than 200 times as long as the shortest waves. Although the actual difference between the extremes is very

small, being one or two ten millionths of a millimeter, their penetrating powers are very different. The shortest can pass through thick sheets of lead, while the longest are absorbed in a few millimeters of tissue. Since this conception of energy in the form of waves is convenient and sanctioned by long usage, it is employed, even by those who believe that energy is actually transmitted in another form.

The second view, which regards the beam as a procession of rapidly moving bundles of energy, prevails in the theories which have been formulated to explain the physical and chemical changes which can be demonstrated in living cells. Quanta differ from each other in their energy content, for this depends on their vibration frequency (the reciprocal of the wave-length), which for gamma rays is very great, while for light waves it is very small. The proportion between the two is of the order of half a million to one. When they strike the atoms of protoplasm they give up some or all of their energy, and it is this transformed energy which initiates the physical and chemical changes.

To understand how this transformation takes place we must picture the atom as made up of a nucleus around which are rotating at enormous velocities a number of negatively charged electrons, some in orbits close to the nucleus and others at greater distances. The former are closely bound and can be dislodged only by a large expenditure of energy such as is found in a quantum of X-rays; the latter, being loosely held, are easily displaced by the small quanta comprising light rays.

Now when a beam of X- or gamma rays strikes a substance composed of such planetary systems, the quanta may chance to pass clean through it without colliding with anything, and emerge on the further side having lost no momentum. Such quanta have no effect and are therefore

without biological interest. But others suffer collisions. When one strikes an inner electron it may knock it from its course to another orbit at a greater distance from the nucleus. In doing this the quantum may give up all of its energy, in which case it ceases to exist. But when such a displacement occurs the atom as a whole acquires energy, for the negative electron can be held by a smaller amount of energy than before. At such a time the atom has a high reactive ability and can enter into chemical combinations which were impossible before. It is in an "excited" condition which lasts for a brief instant, perhaps less than a millionth of a second, for the attractive force of the nucleus is enough to pull the electron back into place. This is the first step in the photochemical process.

The X- and gamma ray quanta possess enough energy to displace an electron from the inner orbit; they may also separate it completely from its atom and send it flying off into surrounding space. This electron is in reality a beta ray since, like the beta rays of radium, it is a negatively charged particle. It is also a cathode ray. Wilson (1118) has photographed these photoelectrons, or rather, the water vapor which condenses on them, and shows that the X-ray beam itself is invisible; its presence can be detected only by the ionization which it produces.

The number of these primary beta rays is not large in comparison with the total number of electrons in the substance traversed by the beam, but they produce indirectly a very considerable effect. Each one, while traveling at high speed, may knock off other electrons or displace them before it comes to rest, so that actually it produces a large amount of ionization. "The absorption of one quantum of 160 KV X-ray is much like a highly localized burst of ionic shrapnel, in which

about 4000 ion pairs are liberated in less than a millionth of a cubic centimeter."

(20) These secondary electrons travel but a short distance and give up their energy in the cell in which they arise.

In this discussion the quantum has been represented as giving up all of its energy at the moment of collision when it sets free a photoelectron. But this does not always occur. A quantum of hard X-ray may strike an electron, displace it, and still retain a considerable portion of its momentum. Because of the collision its course may be changed; it may be scattered through any angle. Most of the quanta continue forward, some are thrown to one side, and some return in the direction from which they have come. Such scattered quanta now collide again and again with electrons, each time setting one free or displacing it, until they have so little energy left that they cannot affect even the electrons of the outer ring. This phenomenon was first investigated by Compton (19), who measured the loss in frequency, or in the other terminology, the increase in wave-length of the deflected rays. The amount of increase varies with the angle of scattering, being greatest at 180° . Biologically these rays, especially those scattered through wide angles, are of greatest importance, for they increase the effectiveness of the beam by as much as 40 per cent if the area and volume of the scattering medium is large. From X-rays produced at low voltages the back scatter is not great; nor is it from very hard X-rays. In this case most of the rays are scattered forward (78).

Radiation quanta produce effects only when their energy is absorbed, that is, when it is imparted to the electrons in the absorbing substance. The amount of ionization produced by a beam of definite hardness is the same for all tissues, and this is parallel to the amount produced

in air by the same beam. For this reason the amount of air ionization is taken as a measure of the ionization which occurs in tissues under the same conditions. This can be measured by appropriate apparatus.

These are some of the elementary principles on which the theories of the action of short radiations on protoplasm are based. Briefly, the change in the molecules of living matter is produced by the displacement or removal of electrons under the impact of energy quanta. This results in a disturbance of the electrical balance, that is, an "excited" condition in which chemical transformations may occur. This is the first step. The second is taken when the excited molecule or atom collides with another. The result of this event may be a molecular breakdown, a process which perhaps is the first of a series of changes which terminate in a very considerable chemical transformation. What these chemical changes are is still unknown.

One theory which is based on these physical assumptions is the Point Heat hypothesis, put forward by Dessauer (26). In their opinion, the major part of the energy absorbed by tissue is transformed into heat. That is, when an excited molecule meets an inactivated one, the displaced electron returns to its original orbit and the energy which is given off in the process is imparted to the colliding molecule in the form of movement. Thus heat is generated and there is a rise in temperature at the point of collision. Dessauer has calculated that the protoplasm in the immediate vicinity may attain a temperature of 100°C ., a point well above the coagulating temperature. As a result, many minute areas of dead matter are formed, and these, when decomposing, set free poisonous substances which produce typical X-ray injuries.

Holthusen (47) criticizes this idea on

the ground that while heat is undoubtedly developed, the amount is actually too small to have any biological effect. By experiment he determined the length of exposure to a high temperature necessary to produce in *Ascaris* eggs the same amount of injury that a dose of 600 Roentgen units produces. The heat energy was so much in excess of what the X-rays could possibly generate that he concludes that the theory is untenable. Holthusen himself believes that the chief effect of the rays is due to the molecular decomposition produced by the secondary electrons.

Another hypothesis is based on the behavior of the colloids when their electrical charges are altered by the displacement of negative electrons. In colloidal solutions there is a difference of potential between the particles and the fluid in which they are suspended. When this is disturbed the particles are precipitated (10). Schinz (95), in a general review of X-ray problems, objects to this on the ground that while such precipitation actually can be seen *in vitro* the doses necessary to produce it are so large that it could not occur under therapeutic conditions. But in the living cell such changes can take place more readily than in a test tube. In all probability this change in the electrical balance is not the only reason for the change in the state of the colloids; they are undoubtedly altered in other ways, although at present this has not been demonstrated.

A change in the electric charge may also serve to alter other physico-chemical conditions of the cell, such as the viscosity, the surface tension, the hydrogen ion concentration, etc. (53). How far these hypotheses may serve to explain the biological effects of radiations remains to be seen. But they are an advance over the older theories in that they are based on a physical foundation.

VII

APPLICATION OF PHYSICAL THEORY TO
BIOLOGICAL PROBLEMS

The quantum theory has very recently been employed by physicists to explain the wide variation in response to radiations in a population which is supposedly homogeneous. This variation is familiar to those who have observed the action of injurious agents of various kinds on cells and organisms. If the percentage of individuals that survive be plotted against the length of exposure to some agent the points will fall along an S-shaped curve, whose course is characteristic for each kind of organism. Four examples are given in Figure 1. That of *Ascaris* eggs (125) is practically symmetrical; the *Drosophila* egg curve differs from it in that the lower portion is much less steep (79). This means that after prolonged doses there is still a considerable proportion of eggs that remains alive. The curve for the protozoan *Colpidium* (21) shows that a long exposure must be given before any cell dies; then the death rate rises rather suddenly, as shown by the steepness of the slope. The carcinoma curve has the same general characteristics but differs in some respects from the others (120). The data were obtained in experiments with finely minced tumor tissue which was first radiated and then inoculated into healthy animals. The curve thus shows what proportion of tumor cells survived the radiation and commenced to grow in the host animal. Each of these four curves is distinct from the others and cannot be confused with them.

When the data on which such curves are based are plotted on logarithmic probability paper they tend to lie along straight lines as shown in figure 2. In this paper "the ordinates are so spaced

that any set of figures which follow the natural law of probability will plot out, not as an ogee curve, but as a straight line" (11). Obviously not all organisms

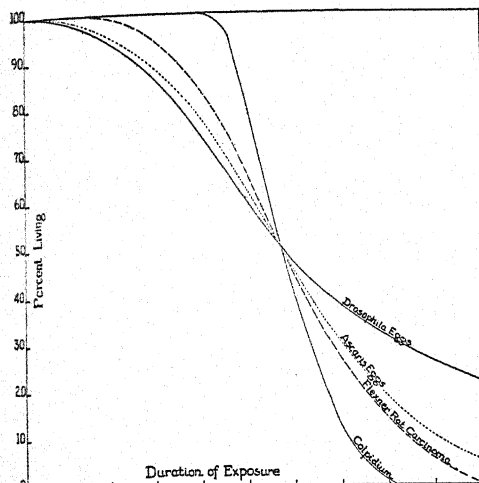


FIG. 1. TYPICAL CURVES SHOWING THE PERCENTAGE OF INDIVIDUALS SURVIVING AFTER EXPOSURE TO RADIATIONS

follow this law perfectly—that is, the frequency distribution of whatever character is being measured is not necessarily symmetrical. But an inspection of the curves given in the figure strongly suggests that it is true in these cases.

Biologists have usually assumed that such curves represent the normal variability in sensitiveness of the individuals to an injurious agent. That is, some are highly susceptible, some are highly resistant, while the majority show medium sensitiveness. But physicists have proposed a very different explanation. Blau and Altenburger (7) assume that there is no biological variability—that every cell or organism in a homogeneous population is like every other in sensitiveness, and that each dies when it has absorbed a sufficient number of X-ray quanta. If all should absorb this number at the same moment, all would die simultaneously.

But, since they do not, the probability is that some may chance to be hit the requisite number of times sooner than others. Thus when a large number of individuals, such as Protozoa, *Drosophila* eggs, or tumor cells are radiated, some die quickly because they have happened to receive the lethal dose soon after exposure begins, while a few others happen to escape for a long time.

Somewhat later, Crowther (21) advanced substantially the same theory and developed it much further. The biological data on which he based his argument he obtained from experiments with *Colpidium*. He states that the course of the mortality curve is to be expected if the cells are killed by a definite number of quantum hits, assuming that the probability of a hit occurring remains constant throughout the exposure. Now a hit must be made, according to his theory, on a small sensitive spot of protoplasm whose nature is such that when it is sufficiently damaged, the cell dies. What this spot may be he does not attempt to determine,

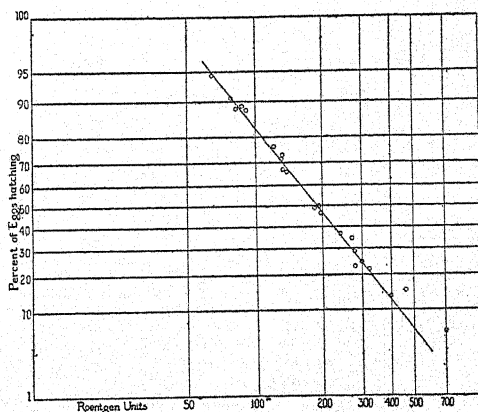


FIG. 2. THE SURVIVAL CURVE OF *DROSOPHILA* EGGS PLOTTED ON LOGARITHMIC PROBABILITY PAPER

but according to his calculations, it is about the size of a nucleus. Assuming this size, he finds that for *Colpidium*, 49 hits must take effect before death occurs.

Now the chance that the sensitive spot will receive this large number of hits in a brief exposure is very small; in other words, no cells die at first, as the curve shows. But after a time most of them will have received, say 40 to 45 hits. Thereafter the chances of receiving the lethal number are great: the cells therefore die at a rapid rate. But a few escape entirely unless the exposure is very intense.

Clark (17) criticizes this application of the quantum theory, showing that in

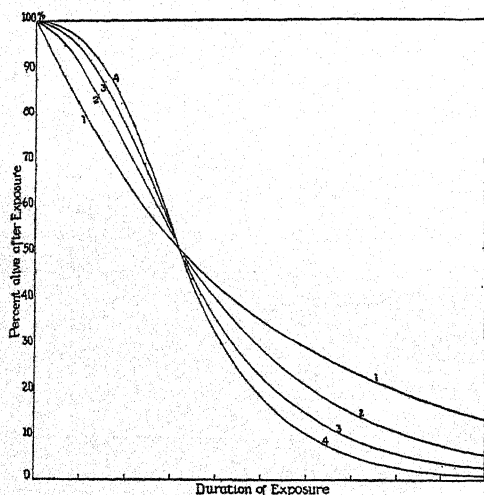


FIG. 3. ILLUSTRATING CONDON AND TERRILL'S VIEW REGARDING THE EFFECT ON THE COURSE OF THE SURVIVAL CURVE OF THE NUMBER OF QUANTA NEEDED TO KILL THE CELL

place of a single spot there is more probably a widely distributed sensitive material which has the property of being changed into a poisonous compound after being struck a sufficient number of times. He remarks that "there is, of course, no good reason for supposing that it is the true explanation of the phenomenon." That is, he recognizes that this type of theory is a formal explanation which does not take into account all of the facts known to radiologists.

The theory is based on the assumption

that all cells are alike in sensitiveness. Crowther, however, states that if they should show variability in this respect, the shape of the survival curve would be the same; that is, the fact of variability would account for its course and not the sensitive spot conception. Biologists cannot accept any theory which leaves out this factor, for no matter how carefully individuals are chosen from a pure line, they will always differ slightly from each other in respect to any character that may be chosen for measurement.

Schinz and Zuppinger (97) have taken this factor into account, and have shown that with slight modifications the sensitive spot theory may still be valid. Indeed, they conclude that the theoretical curve based on their calculations actually fits Crowther's data better than his own. A further step was taken by Condon and Terrill (20), who discuss the consequences which should follow when cells are killed by quanta of different sizes, that is by X-ray beams produced at different voltages. They show that if one large quantum, produced at 190 KV., is sufficient to kill a cell, the mortality curve should have one shape, while if smaller quanta, produced at 100 KV. are employed, more than one will be necessary to bring about the same result, and in such a case, the curve should have a different shape. The results of their calculations are shown in Figure 3. The curves have been drawn so that the abscissas for 50 per cent death coincide. The curve which should result when death is due to one quantum hit slopes steeply down from its point of origin and then turns toward the horizontal; the curve for four quantum hits is at first nearly horizontal, then very steep, and finally almost horizontal.

Experimental evidence which supports this view is given by Holweck and Lacasagne (49), who exposed bacterial cul-

tures to very soft X-rays, the wave lengths being 4.0 and 8.0 Angstrom units. According to their calculations, if one quantum hit of the shorter rays is effective, then four hits of the longer are needed. The sensitive volume corresponds to the volume of the chromatin in ordinary cells.

More evidence is offered by Glocker, Hayer, and Jüngling (37), who irradiated the horse bean, *Vicia faba*, with carefully measured doses of soft (80KV.) and hard (180 KV.) X-rays and determined the percentage of individuals which stopped growing soon after exposure. The courses of the two curves plotted from the data obtained in this way, differ somewhat from each other, a proof, according to the authors, of the differential effect of small and large quanta. When the beans were placed on a large wooden block from which there was a considerable amount of back scatter, the death-rates were much higher than before, because of the additional energy furnished by the recoil electrons. In this experiment the courses of the two curves are nearly alike, and practically the same as one of the preceding curves. Such a result causes one to doubt whether there is any real difference in the curves.

In summary, the theory which has just been outlined rests on the assumption that X-rays produce their effect by means of discrete quantum hits in a sensitive region. The number of hits required depends, aside from the nature of the cell, whether sensitive or resistant, on the size of the quanta. And on this number depends the course of the mortality curve.

In the present state of our knowledge we cannot prove or disprove these assumptions. There can be no question but that cells are killed when they have absorbed a sufficient amount of energy which is given up by the quanta; but whether only

that energy which is absorbed in a definite region such as the nucleus is effective in causing the death of the cell seems very questionable. So close are the interrelations between the nucleus and cytoplasm that we cannot say that injuries to the latter are wholly distinct from injuries to the former. The conclusion of the argument, that the mortality curves should vary with the wave-length, that is, the quantum size, can be put to a practical test.

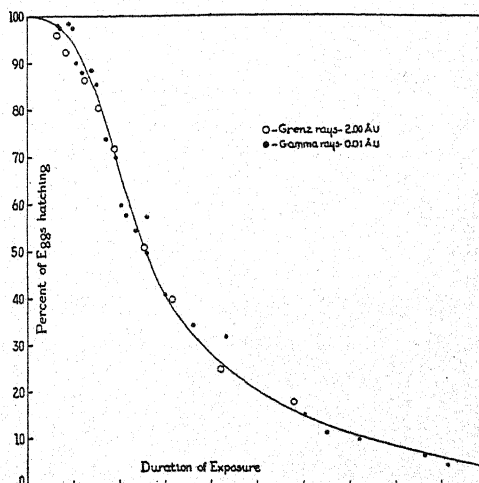


FIG. 4. THE COURSE OF THE SURVIVAL CURVE OF DROSOPHILA EGGS IS NOT AFFECTED BY THE WAVE LENGTH, I.E. QUANTUM SIZE, OF THE RADIATION

To determine this point I have used *Drosophila* eggs (75), exposing them to very short waves of highly filtered gamma rays of radium, and to very long Grenz rays. The former have a wave-length of about 0.01 Angstrom units, representing a voltage of about 1000 KV; the latter have a wave-length of about 1.7 units and are produced at 10 KV. Inasmuch as the quantum size varies with the square of the voltage it is obvious that if size makes a difference in death-rate, it should be very apparent in this test. The results are shown in Figure 4. The data

have been brought together so that the abscissas for 50 per cent killed are the same. The small solid circles show the results of individual tests with gamma rays; the large open circles represent averages of several experiments made with Grenz rays under uniform conditions. The solid curve itself is based on data obtained from numerous experiments with X-rays involving more than 200,000 eggs, made during the past four years. In these the wave-lengths varied from 0.08 to 0.70 Angstrom units. It is obvious that the course of the curve is not changed at all when the wave-length is varied within these very wide limits.

Braun and Holthusen (12) have recently made similar experiments on *Ascaris* eggs and have come to the same conclusion. An important point which they emphasize is that the course of the mortality curve changes somewhat with the length of the dose; that is, there is a time factor which must be considered, the effect of which had previously been investigated by Liechti (62). A dose which kills 50 per cent of the individuals may be given in a short time or over a long period in fractions. In the latter case the development of the eggs is held in check by keeping them under anaerobic conditions. The curve is now flatter than in the first method, and resembles the theoretical curve demanded when large quanta are used. This factor may explain some of the results obtained by other investigators.

This part of the theory, then, is not supported by the results of these extensive experiments. A further difficulty in its acceptance lies in the sudden changes in susceptibility during mitosis. To explain this situation one might postulate that the sensitive spot grows larger during cell division and thus is more likely to be hit; or else that its nature has changed so that it may be destroyed by a variable

number of hits, depending on the stage in mitosis during which irradiation is given. Either possibility introduces a factor which the theory is framed to avoid, namely, variation in the biological material. In its present form it appears untenable, but it is a valuable contribution to radiology, since it calls attention to certain physical conceptions which biologists must take into consideration when attempting to explain the effects of radiations.

VIII

QUANTITATIVE EFFECTS OF DIFFERENT WAVE-LENGTHS

For many years the question of the relative effectiveness of long and short rays has been debated by radiotherapists, who must use both kinds in their work. In skin therapy the long, non-penetrating rays are employed because they give up their energy at the surface; in deep therapy, such wave-lengths are chosen as will penetrate to the desired place. If beams of widely different qualities have the same intensity,—that is, if they produce the same amount of ionization in air,—will their total biological effect be the same or will one be more effective than the other. The question is of great practical importance, for if there is a difference, then the problem of dosage becomes very complicated.

The general opinion has been that long rays are more effective in producing an erythema (119), but recent work shows that this is not strictly true (27). If small areas of skin are exposed to equal doses of long and short rays the amount of reddening is the same in all. This test is not ideal for solving the problem because of the high degree of variability in human patients, and because the depth of the absorbing tissue is necessarily different in the two cases. The long rays

are absorbed in a few millimeters of tissue; the short, in several centimeters. A better method is to use small objects, such as cells, or eggs of *Drosophila* or *Ascaris* in which the question of penetration does not arise.

Dognon (29), who used *Ascaris* eggs, concluded that moderately soft rays are least effective, while rays both shorter and longer than these are more potent. Some doubt is thrown on these results by Dauvillier (25), who shows that Dognon's computations of the intensity of the beams were wrong. Zuppinger (125), who reviews the subject at length, comes to somewhat the same conclusion as Dognon, but finds that the increase in effectiveness of the very long rays is slight. On the other hand Bolaffio (9) arrives at the opposite conclusion, for he reports that long waves are more effective than the short.

Some of these discordant results are almost certainly due to inadequate methods of measuring intensities at widely different wave-lengths. The ionization chambers which were used were not accurate throughout the entire range, registering too low at some points and too high at others. When, however, measurements are made with a large, open, air ionization chamber of the type now recognized as free from these errors, the biological effect of beams of different qualities is found to be the same.

This was first clearly demonstrated by Wood (121, 122), who used as a test object finely minced tumor tissue which after irradiation was inoculated into healthy animals. The criterion of effect was the percentage of "takes." If no tumors grew after inoculation the cells had received a lethal dose. In all of the many tests with different tumor strains the conditions of exposure were carefully regulated so as to ensure perfect constancy

of output from the tube. For example, the current was continuous, not fluctuating as in the case of machines having mechanical rectification. The two beams used for experiment were nearly homogeneous in wave-length (0.68 and 0.22 A. U.). The results show that when the tumor cells of any particular strain are exposed to these qualities of radiation, the doses varying from subminimal to lethal, the proportion of takes which re-

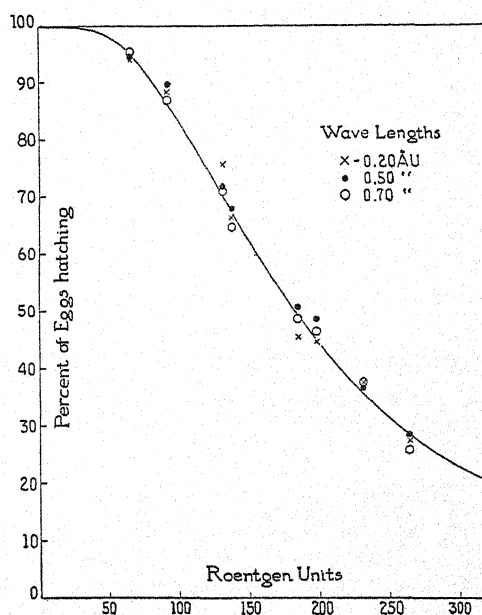


FIG. 5. AN EXPERIMENT SHOWING THAT X-RAYS OF DIFFERENT WAVE LENGTH ARE EQUALLY EFFECTIVE BIOLOGICALLY

sult lie along a single curve. In other words, the biological effect is correlated with the degree of ionization as measured in air. And since this is practically the same as in tissue, the conclusion must be drawn that the amount of ionization in tissues determines the amount of effect, regardless of wave-length.

Subsequently I repeated these experiments (75), using *Drosophila* eggs in place of tumor cells, and employing a third wave-length intermediate between

the two used by Wood. While the sensitiveness of these eggs is far greater than that of any of the various kinds of tumor cells,—to reduce the number of takes to 50 per cent requires from six to eleven times as many Roentgen units as to kill half of a sample of *Drosophila* eggs,—they reacted in the same way. Equal doses, measured by the large ionization chamber, kill equal proportions of eggs. Holthusen (46) comes to the same conclusion after previously stating that the reverse was probably true.

Further confirmation is furnished by quantitative measurements of chemical reactions. Fricke and his co-workers have found that the amount of oxyhemoglobin which is transformed into methemoglobin (33), and of ferrous sulphate which is oxidized by the radiations (34) is independent of the wave-length employed. More recently Quimby and Downes (84) report that this is true also for the precipitation of mercurous chloride from Eder's solution.

This being the case, the experiment may be reversed; the quantitative effect can be used as a measure of the dose. For example, if a large number of *Drosophila* eggs is exposed to a beam of unknown intensity for ten minutes, and if, as a result, half of the individuals fail to hatch, then 180 Roentgen units must have been delivered at the rate of 18 r/min. (76). Many tests made during the past few years have shown that a carefully measured dose of this size always gives this result, the variation being less than 5 per cent. In the same way Quimby and Downes (84) use their chemical method and find that the results when compared with ionization tests are correct within a few per cent.

Reasonably precise measurement of dosage is essential in any experiments regardless of whether they are quantitative in nature or otherwise. Without it, one can never be certain that the dose he gives is really what he supposes it to be; and for another to repeat the work accurately is almost impossible. The older methods of defining dosage by stating the voltage, filtration, and amperage are of very restricted value because different machines differ so widely in their output even when these factors are supposedly the same. This is because the current in some is interrupted, in others it is nearly continuous; because the output of tubes varies with their age and the thickness of the glass; because the meters are by no means accurate; and because the intensity of the beam varies within wide limits, depending on the way in which the control board resistance is adjusted (79).

Fortunately it is possible now to measure intensities with ease and with fair accuracy (13), and to determine the number of Roentgen units delivered during exposure. When this information is given, together with the voltage and filtration, anyone may obtain the same dose on another machine. The mention of the latter data is important, not because the effects of the primary beam vary with the different qualities but because the penetration varies and so also does the amount of back-scattered radiation.

The accurate measure of dosage in Roentgen units reduces the number of variable factors in the experiment. One which cannot now be excluded is that of biological variation; but if this is measured properly and taken into account, sound conclusions may be drawn regarding the effect of radiations on living matter.

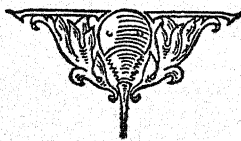
LIST OF LITERATURE

- (1) ALBERTI, W., and G. POLITZER. 1924. Über den Einfluss der Roentgenstrahlen auf die Zelltheilung. *Arch. mikro. Anat.*, 100: 83.
- (2) ANCEL, S. 1924. Action de faibles doses de rayons X sur des graines sèches. *Compt. Rend. Soc. Biol.*, 91: 1435.
- (3) ARNTZEN, L., and C. KREBS. 1925. Investigation into the biological effect of filtered and unfiltered rays. *Acta Radiologica*, 4: 5.
- (4) BERGONIE, J., and L. TRIBONDEAU. 1906. Interprétation de quelques résultats de la radiothérapie. *Compt. Rend. Acad. Sci.*, 143: 983.
- (5) BERSA, E. 1927. Strahlenbiologische Untersuchungen, II. *Sitz. Akad. Wiss. Wien*, 136: 383.
- (6) BISCEGLIE, V., and G. BUCCIARDI. 1929. Le modificazioni funzionali e strutturali degli espianti di cuore embrionale di pollo sottoposti all'azione di sostanze radioattive. *Arch. Exp. Zellforsch.*, 7: 444.
- (7) BLAU, M., and K. ALTENBURGER. 1922. Über einige Wirkungen von Strahlen. *Zeitschr. f. Physik.*, 12: 315.
- (8) BLUMENTHAL, R., and M. M. D. WILLIAMS. 1928. Effects of radium radiations on the oxygen consumption of grasshopper eggs. *Anat. Rec.*, 41: 45.
- (9) BOLAFFIO, M. 1925. Versuche zur luftelektrischen und biologischen Wirkung von Strahlen verschiedener Wellenlänge. *Strahlentherapie*, 20: 673.
- (10) BORDIER, H. 1913. Biochemische Wirkung der Strahlen. *Strahlentherapie*, 2: 368.
- (11) BOVIE, W. T. 1926. Law of relation between exposure and the biological effect of radiation. *J. Cancer Res.*, 10: 161.
- (12) BRAUN, R., and H. HOLTHUSEN. 1929. Einfluss der Quantengröße auf biologischen Wirkung verschiedener Roentgenstrahlenqualitäten. *Strahlentherapie*, 34: 707.
- (13) BRAUN, R., and H. KUSTNER. 1929. Die Harteabhängigkeit der technische Fingerhutmammern. *Strahlentherapie*, 33: 551.
- (14) CANTI, R. G., and M. DONALDSON. 1926. Effects of radium on mitosis in vitro. *Proc. Roy. Soc. B*, 100: 283.
- (15) CANTI, R. G., and F. G. SPEAR. 1929. Effect of gamma irradiation on cell division in tissue culture in vitro. *Proc. Roy. Soc. B*, 105: 93.
- (16) CASPARI, W. 1928. Biologische Grundlagen der Strahlenbehandlung bösartiger Geschwülste. *Handb. ges. Strahlenheilkunde*. I. J. F. Bergmann, München.
- (17) CLARK, H. 1927. A theoretical consideration of the action of X-rays on *Colpidium colpoda*. *J. Gen. Physiol.*, 10: 623.
- (18) COLWELL, H. A., and S. RUSS. 1924. Radium, X-rays, and the Living Cell. Bell and Son, London.
- (19) COMPTON, A. H. 1926. X-rays and Electrons. Van Nostrand, New York.
- (20) CONDON, E. U., and H. M. TERRILL. 1927. Quantum phenomena in the biological action of X-rays. *J. Cancer Res.*, 11: 324.
- (21) CROWTHER, J. A. 1926. The action of X-rays on *Colpidium colpoda*. *Proc. Roy. Soc. B*, 100: 390.
- (22) CURTIS, W. C. 1928. Old problems and a new technique. *Science*, 67: 141.
- (23) CZEPA, A. 1924. Das Problem der wachstumsfördernden und funktionssteigernden Roentgen- und Radiumwirkung. *Strahlentherapie*, 16: 913.
- (24) DALCQ, A. 1930. Interpretation cytologique des effets sur la gastrulation, de l'irradiation d'un des gamètes chez *Rana fusca*. *Compt. Rend. Soc. Biol.*, 104: 1055.
- (25) DAUVILLIER, A. 1925. Sur l'action biologique des rayons X de diverses longueurs d'onde. *Compt. Rend. Acad. Sci.*, 181: 1130.
- (26) DESSAUER, F. 1924. Über die biologische Strahlenwirkung. *Fort. Roentgenol.*, 32: 319.
- (27) DETERMANN, A., H. JACOBI, and H. HOLTHUSEN. 1927. Die Erythemwirkung verschiedener Strahlenqualitäten. *Strahlentherapie*, 26: 472.
- (28) DOBZHANSKY, T. 1929. Genetical and cytological proof of translocations involving the third and fourth chromosomes of *Drosophila melanogaster*. *Biol. Zentralbl.*, 49: 408.
- (29) DOGNON, A. 1925. La mesure et l'action biologique des rayons X de différentes longueurs d'onde. *Archiv. phys. Biol.*, 4: 87.
- (30) FAIRBROTHER, J. A. V. 1928. Note on viscosity changes produced in egg albumen by X-rays. *Brit. J. Radiol.*, 1: 125.
- (31) FALTA, W., and G. SCHWARZ. 1911. Wachstumsförderung durch Radiumemanation. *Berl. kl. Wchnschr.*, 1: 605.
- (32) FLASKAMP, W. 1930. Über Roentgenschäden und Schäden durch radioaktive Substanzen. Sonderband zur Strahlentherapie, 12.
- (33) FRICKE, H., and S. MORSE. 1927. Action of roentgen rays on solutions of ferrosulphate in water. *Am. J. Roent.*, 18: 426.

- (34) FRICKE, H., and B. W. PETERSON. 1927. Action of roentgen rays on solutions of oxyhemoglobin in water. *Am. J. Roent.*, 17: 611.
- (35) GANS, O. 1923. Über die Gewebsatmung in gesunden und kranken Haut. *Deutsche med. Wchnschr.*, 49: 16.
- (36) GASSUL, R. 1925. Einfluss der Strahlenenergie auf die lebende Zelle in vitro (in Russian). *Abs. in Zeit. ges. Radiologie*, 1926: 1. 595.
- (37) GLOCKER, R., E. HAYER, and O. JÜNGLING. 1929. Über die biologische Wirkung verschiedener Roentgenstrahlenqualitäten bei Dosierung in R Einheiten. *Strahlentherapie*, 32: 1.
- (38) HALBERSTÄDTER, L., and A. SIMONS. 1922. Zum Problem der Reizwirkung der Roentgenstrahlen. *Fort. Roent.*, 28: 499.
- (39) HASTINGS, S., H. BECKTON, and B. H. WEDD. 1912. Effect of radiation on silkworms. *Arch. Middlesex Hosp.*
- (40) HEILBRUNN, L. V. 1927. The viscosity of protoplasm. *QUART. REV. BIOL.*, 2: 230.
- (41) HEINECKE, H. 1914. Zur Theorie der Strahlenwirkung. *Münch. med. Wchnschr.*, 807.
- (42) HERTWIG, G. 1911. Radiumbestrahlung unbefruchteter Froscheier und ihre Entwicklung nach Befruchtung mit normalen Samen. *Arch. mikro. Anat.*, 77: 165.
- (43) HERTWIG, O. 1911. Die Radiumkrankheit tierscher Keimzellen. *Arch. mikro. Anat.*, 77: 1.
- (44) HOFFMANN, V. 1922. Über Erregung und Lähmung tierischer Zellen durch Roentgenstrahlen. *Strahlentherapie*, 13: 283.
- (45) HOLTHUSEN, H. 1921. Beiträge zur Biologie der Strahlenwirkung. *Arch. ges. Physiol.*, 187: 1.
- (46) ———. 1926. Der derzeitige Stand der physikalischen Messmethoden. *Strahlentherapie*, 22: 1.
- (47) ———. 1927. Der Grundvorgang der biologischen Strahlenwirkung. *Strahlentherapie*, 25: 157.
- (48) ———. 1929. Die biologische Dosierung in der Strahlentherapie der einzelnen Gewebe. *Handb. ges. Strahlenheilkunde*. J. F. Bergmann, München.
- (49) HOLWECK, F., and A. LACASSAGNE. 1930. Sur le mécanisme de l'action cytocaustique des radiations. *Compt. Rend. Soc. Biol.*, 103: 766.
- (50) IVEN, H. 1925. Neuere Untersuchungen über die Wirkung der Roentgenstrahlen auf Pflanzen. *Strahlentherapie*, 19: 413.
- (51) JANNSON, G. 1927. Die Einwirkung der Roentgenstrahlen auf das Zellprotoplasma. *Acta Radiologica*, 8: 427.
- (52) JÜNGLING, O. 1920. Die praktische Verwendbarkeit der Wurzelreaktion von *Vicia faba* zur Bestimmung der biologischen Wertigkeit der Roentgenstrahlen. *Münch. Wchnschr.*, 1141.
- (53) KARCZAG, L. 1928. Strahlung und Kolloide. *Handb. ges. Strahlenheilkunde*. J. F. Bergmann. München.
- (54) KARCZAG, L., G. v. KARKAS, and G. GRÖRGYI. 1927. Über die biologische Indifferenz der Roentgenstrahlen gegenüber künstlichen Gewebeskulturen. *Arch. Exp. Zellforsch.*, 4: 206.
- (55) KIMURA, N. 1919. Effects of X-rays on living carcinoma and sarcoma cells in vitro. *J. Cancer Res.*, 4: 95.
- (56) KNIPPING, H. W., and H. L. KOWITZ. 1924. Über die Einfluss der Roentgenstrahlen auf die Eiweisskörper des Plasmas. *Fort. Roentgenol.*, 31: 660.
- (57) KÖRNICKE, H. 1915. Über die Wirkung verschiedener starker Roentgenstrahlen auf Keimung und Wachstum bei den höheren Pflanzen. *Jahrb. wiss. Botan.*, 56: 416.
- (58) KOVACS, K. Der Einfluss der Roentgenstrahlen auf die Diffusions- und Durchlässigkeit der Zellmembran. *Strahlentherapie*, 30: 77.
- (59) LAZARUS-BARLOW, W. S., and H. BECKTON. 1913. Radium as a stimulus of cell division. *Arch. Middlesex Hosp.*, 12: 47.
- (60) LEPESCHKIN, W. W. 1930. My opinion about protoplasm. *Protoplasma*, 9: 293.
- (61) LEWIS, W. H., and M. R. LEWIS. 1924. Behavior of cells in tissue cultures. *General Cytology*. Univ. Chicago Press.
- (62) LIECHTI, A. 1929. Über den Zeitfaktor der biologischen Strahlenwirkung. *Strahlentherapie*, 33: 1.
- (63) LOEB, L. 1922. Effects of Roentgen rays and radioactive substances on living cells and tissues. *J. Cancer Res.*, 7: 229.
- (64) MARKOWITS, E. 1922. Cytologische Veränderungen der Einzeller *Paramecium* nach Bestrahlung mit Mesothorium. *Arch. Zellforsch.*, 16: 238.
- (65) MAJOR, J. W. 1924. The production of non-disjunction by X-rays. *J. Exp. Zool.*, 39: 381.
- (66) ———. 1927. Comparison of susceptibility to X-rays of *Drosophila* at various stages of its life cycle. *J. Exp. Zool.*, 47: 63.

- (67) MOTTRAM, J. C. 1913. Action of beta and gamma rays of radium on the cell in different states of nuclear division. *Arch. Middlesex Hosp.*, 12: 98.
- (68) MULLER, H. J. 1928. The production of mutations by X-rays. *Proc. Nat. Acad. Sci.*, 14: 714.
- (69) ———. 1930. Radiation and genetics. *Am. Nat.*, 64: 220.
- (70) NADSON, G. A. 1925. Über die Primärwirkung der Radiumstrahlen auf die lebendige Substanz. *Biochem. Zeit.*, 155: 381.
- (71) NASSET, E. C., and C. A. KOFOID. 1928. Effects of radium on *Endamoeba dysenteriae* in vitro. *Univ. Calif. Pub.* 31: 387.
- (72) PACKARD, C. 1916. Effect of radium radiations on the rate of cell division. *J. Exp. Zool.*, 21: 199.
- (73) ———. 1918. Effect of radium radiations on the development of *Chaetopterus*. *Biol. Bull.*, 35: 50.
- (74) ———. 1924. Susceptibility of cells to radium radiations. *Biol. Bull.*, 46: 165.
- (75) ———. 1927. Quantitative biological effects of X-rays of different wave lengths. *J. Cancer Res.*, 11: 1.
- (76) ———. 1927. A biological measure of X-ray dosage. *J. Cancer Res.*, 11: 282.
- (77) ———. 1929. Relation of wave length to the death rate of *Drosophila* eggs. *J. Cancer Res.*, 13: 87.
- (78) ———. 1929. The biological measure of scattered radiation. *J. Cancer Res.*, 13: 373.
- (79) ———. 1930. Biological calibration of an X-ray dosimeter. *J. Cancer Res.*, 14: 134.
- (80) ———. 1930. Relation between division rate and the radiosensitivity of cells. *J. Cancer Res.*, 14: 359.
- (81) PETRY, E. 1922. Zur Kenntnis der Bedingungen der biologischen Wirkung der Roentgenstrahlen. *Biochem. Zeit.*, 128: 326.
- (82) PRIME, F. 1916. Action of radium on embryo heart muscle. *Proc. N. Y. Path. Soc.*, 16: 56.
- (83) ———. 1917. Observations on effects of radium on tissue growth in vitro. *J. Cancer Res.*, 2: 107.
- (84) QUIMBY, E. H., and H. R. DOWNES. 1930. A chemical method for the measurement of quantity of radiation. *Radiology*, 14: 468.
- (85) RAJEWSKY, B. 1928. Die Strahlungsreaktion des Eiweisses und die Erythemawirkung. *Strahlentherapie*, 29: 759.
- (86) REDFIELD, A. C., and E. M. BRIGHT. 1922. Effects of radium rays on metabolism and growth in seeds. *J. Gen. Physiol.*, 4: 297.
- (87) REGAUD, C. 1923. A propos de la durée d'application en curietherapie et sur la valeur pratique de l'index karyokinétique. *Bull. de l'Assoc. franc. pour l'étude du Cancer*, 12: 482.
- (88) REGAUD, C., A. LACASSAGNE, and J. JOVIN. 1925. Lésions microscopiques déterminées par les Rayons X dans l'embryon de poulet. *Compt. Rend. Soc. Biol.*, 93: 1587.
- (89) REISS, P. 1925. Sur l'excitation des bourgeons de plantes par Rayons X. *Compt. Rend. Soc. Biol.*, 92: 984.
- (90) RICHARDS, A. 1914. Effect of X-rays on the rate of cell division in early cleavage of *Planorbis*. *Biol. Bull.*, 27: 67.
- (91) ———. 1915. Experiments on X-radiation as a cause of permeability changes. *Am. J. Physiol.*, 36: 400.
- (92) RIEDER, H., and J. ROSENTHAL. 1928. *Lehrbuch der Roentgenkunde*, III. Leipzig.
- (93) ROGERS, C. G., and K. S. COLE. 1925. Heat production by the eggs of *Arbacia punctulata* during fertilization and early cleavage. *Biol. Bull.*, 49: 338.
- (94) SCHAUDINN, F. 1899. Über den Einfluss der Roentgenstrahlen auf Protozoen. *Arch. ges. Physiol.*, 77: 29.
- (95) SCHINZ, H. R. 1924. Grundfragen der Strahlentherapie. *Klin. Wchnschr.*, 2: 2349.
- (96) SCHINZ, H. R., and M. SŁOTOPOLSKY. 1925. Die Roentgenhoden. *Ergebn. d. med. Strahlenforsch.* I.
- (97) SCHINZ, H. R., and A. ZUPPINGER. 1928. Probleme der allgemeinen Strahlenbiologie. *Klin. Wchnschr.*, 1070.
- (98) SCHWARZ, G. 1903. Über die Wirkung der Radiumstrahlen: eine physiologische-chemische Studie am Hühnerei. *Arch. f. Physiol.*, 100: 532.
- (99) ———. 1926. Über die Latenzzeit. *Acta Radiologica*, 7: 452.
- (100) SCHWARZ, G., A. CZEPA, and L. SCHINDLER. 1924. Zur Problem der wachstumsfördernden Reizwirkung des Roentgenstrahlen bei höheren Pflanzen. *Fort. Roent.*, 31: 665.
- (101) SHEARER, C. 1922. On the oxidation processes in the fertilization of the Echinoderm egg. *Proc. Roy. Soc. B*, 93: 213.
- (102) STEPHAN, R. 1920. Über die Steigerung der Zellfunktion durch Roentgenenergie. *Strahlentherapie*, 11: 517.
- (103) STOKLASA, J. 1914. Bedeutung der Radioaktivität in der Physiologie. *Strahlentherapie*, 4: 1.
- (104) STRANGEWAYS, T. S. P., and H. B. FELL. 1927. A study of the direct and indirect action of

- X-rays upon the tissues of the embryonic fowl. *Proc. Roy. Soc. B*, 102: 9.
- (105) STRANGEWAYS, T. S. P., and F. L. HOPWOOD. 1926. Effect of X-rays upon mitotic cell division in tissue cultures in vitro. *Proc. Roy. Soc. B*, 100: 283.
- (106) VINTEMBERGER, P. 1928. Sur les variations de la radiosensibilité au cours des premières mitoses de segmentation dans l'oeuf de *Rana fusca*. *Compt. Rend. Soc. Biol.*, 98: 536.
- (107) ———. 1928. Sur l'emploi des rayons X en embryologie comme agents de destruction localisée. *Compt. Rend. Soc. Biol.*, 99: 1590.
- (108) ———. 1929. Sur les effets d'applications de rayons X localisées soit au protoplasme, soit à la région nucléaire. *Compt. Rend. Soc. Biol.*, 99: 1968.
- (109) WAIL, S. S., and J. G. LIBERSON. 1926. Über die Wirkung der Roentgenstrahlen auf die Protoplasmastruktur während der sog. latent Period. *Centr. f. allg. Path. und path. Anat.*, 37: 247.
- (110) WARREN, S. L. 1928. Physiological effects of Roentgen radiation upon normal body tissues. *Physiol. Rev.*, 8: 92.
- (111) WEBER, F. 1922. Frühtreiben ruhender Pflanzen durch Roentgenstrahlen. *Biochem. Zeit.*, 128: 495.
- (112) ———. 1923. Roentgenstrahlenwirkung und Protoplasmaviscosität. *Arch. ges. Physiol.*, 198: 644.
- (113) WELS, P. 1924. Die bisherigen kolloidchemischen Untersuchungen über Wirkungen der Roentgenstrahlen. *Fort. Roent.*, 15: 112.
- (114) ———. 1924. Der Einfluss der Roentgenstrahlen auf die Oxidationsgeschwindigkeit in Zellen. *Arch. ges. Physiol.*, 203: 262.
- (115) WERNER, R. 1911. Über die chemische Imitation der Strahlenwirkung. *Strahlentherapie*, 1: 442.
- (116) WILLIAMS, M. 1923. Observations on the action of X-rays on plant cells. *Ann. Bot.*, 37: 217.
- (117) ———. 1925. Some observations on the action of radium on certain plant cells. *Ann. Bot.*, 39: 547.
- (118) WILSON, C. T. R. 1912. Apparatus for making visible the tracks of ionizing particles in gases. *Proc. Roy. Soc. A*, 87: 277.
- (119) WINTZ, H., and W. RUMP. 1926. Biologische Wirkung verschiedener Roentgenstrahlenqualitäten. *Strahlentherapie*, 22: 451.
- (120) WOOD, F. C. 1924. Effect on tumors of radiations of different wave lengths. *Am. J. Roent.*, 12: 474.
- (121) ———. 1925. Further studies in the effectiveness of different wave lengths of radiation. *Radiology*, 5: 199.
- (122) WOOD, F. C., and F. PRIME. 1915. Action of radium on transplanted tumors of animals. *Ann. Surgery*, 62: 751.
- (123) ——— and ———. 1919. Action of X-rays on tumors. *J. Cancer Res.*, 4: 49.
- (124) ZUELZER, M., and E. PHILIPP. 1925. Beeinflussung des kolloidalen Zustandes des Zellinhaltes von Protozoen durch Radiumstrahlen. *Strahlentherapie*, 20: 787.
- (125) ZUPPINGER, A. 1926. Radiobiologische Untersuchungen an Ascarisiern. *Strahlentherapie*, 28: 639.





QUANTITATIVE RELATIONS IN BIOLOGICAL PROCESSES AND THE RADIATION HYPOTHESIS OF CHEMICAL ACTIVATION

By CHARLES D. SNYDER

Professor of Experimental Physiology, The Johns Hopkins University, Baltimore, Md.

I

THE PROBLEM

CORRELATION between photochemical reactions and Planck's quantum theory of radiant energy has been the subject of many investigations since that early work of Stark in 1909, of Einstein in 1912, and the experiments of E. Warburg in 1912 and M. Bodenstein in 1913 (1). It was a natural next step to investigate the phenomena of photochemical reactions occurring among living things (2); and when once the idea became clear, that wherever reaction is caused by radiant energy of any kind there probably will be reaction per quantum, determined by the frequency of the absorbed radiation, then a widespread search got under way for the correlations between atomic and molecular exchanges and the quanta of non-luminous, or thermal, radiations. Trautz (1906-1918); Haber, 1911; Baly, 1913; Perrin, 1919; W. C. M. Lewis, 1919; G. N. Lewis and D. F. Smith, 1925; Tolman, 1925, and others made important contributions to the facts and theory in this very interesting field of chemistry (3).

The difficulties of applying the quantum theorem to chemical reactions that proceed in condensed systems have been considerable; the difficulties in its application to heterogeneous systems, to colloidal suspensions in liquids, must be accordingly all the greater. There would seem to be

no way to measure either emitted, incident or absorbed radiation in systems where the source of radiation, as well as the absorption, is within the system itself. In the study of photochemical processes in living matter the source of light in most cases can be controlled, and the quantity absorbed in many cases can be measured; and while no demonstration has been made of the direct validity of the equivalence law, yet the relations between molecular and quantal exchanges that have been shown in these investigations are of the greatest interest, and suggest further that similar studies of darkfield or non-luminous reactions in living matter may yield results of no less interest. The measure of molecular exchanges in such systems has offered comparatively little difficulty. As for the measure of quanta the difficulty is obvious and every method will meet serious objection (4). But as a preliminary working hypothesis we may assume that during a physiological action all or an aliquot part of the radiational energy exchanges have their counterpart in the form of external work, or in heat, or both; the work and heat may be observed by appropriate methods.

Finally either an arbitrary value may be assigned to the unknown frequency characteristic, or the frequency may be calculated from the reverse statement of the law of equivalence. In the former case the frequency is assumed from Wien's law of displacement and the quanta are calcu-

lated; in the latter case the ratio of quanta to number of activated molecules is assumed to be unity, the calculated frequency from which is compared with that demanded by theory.

As to the possibility of the law of quanta holding among physiological processes one need only recall the Weber-Fechner law of stimulation. This "law" was based upon the observation that increasing stimuli have increasing effects only when the energy of the increased stimulus has reached a certain new level, in other words that stimuli are effective in jumps rather than in continuous gradations. The all-or-none law among physiological processes in last analysis likewise may turn out to have its final explanation in the theory of quanta (Pratt and Eisenberger, 2). Indeed Zwaardemaker (2, 1927, p. 252) urges the reinvestigation of this class of phenomena from the viewpoint of the quantum theorem and the radiational hypothesis as being well worthwhile.

In the explanation of the sensitizing action of some dyes, as developed by von Tappeiner (2), it is assumed that ultra violet frequencies are somehow emitted and act on the absorbing protoplasm. Gurwitsch (2) explains his observations of increased mitosis and cell division in one growing root-tip, when near another growing tip, by assuming that radiant energy, sent out from the one tip, is absorbed by the other. Finally the radioactive phenomena as observed by Zwaardemaker (2) in his long series of researches all suggest that living matter is continually under the influence of radiations of many sorts that from time to time take on effective or critical frequencies.

After this essay was practically completed a title indicating a similar study came to my attention, namely, the dissertation of L. B. Becking (2) on

"Radiation and Vital Phenomena," a copy of which finally came into my hands. In this work the author has examined some physiological reactions, especially those that are influenced by both light and heat, and finds that the calculated wave-length often corresponds to the incident wave-length optimal for the process, or to the wave-length of maximum absorption by the proteins involved in the tissue observed. The treatise rather fully describes the equations underlying the applications of the radiational hypothesis to chemical reactions, following the reasoning of Ornstein, Perrin and Tolman. When the rates of reaction at different temperatures are the data used in calculating the energy transfer, the equation of Perrin,

$$\text{namely, } \lambda = \rho \cdot \frac{6.2}{T_1(T_1 + 10) \log_{10} Q_{10}} \text{ is employed,}$$

where 6.2 is the product of a number of radiation constants and ρ is Perrin's constant, which is made equal to 1 for cases where the usual temperature coefficients hold, and < 1 for cases where the higher coefficients obtain ($\rho = 0.27$ in Becking's cases!) and then called a modification constant. Q_{10} is the usual temperature coefficient of rate of reaction for temperatures 10° apart.

The above equation has its fundamental derivation in (a) Planck's luminosity equations and (b) in the van't Hoff-Arrhenius equation for influence of temperature on chemical reaction rates. For it has been shown theoretically (Trautz, Marcelin, Rice, Lewis, Perrin, Tolman) that for cases where light is absorbed (a) may be written finally

$$\ln q = \rho \frac{h\nu}{k} \left(\frac{1}{T_1} - \frac{1}{T_2} \right) \quad (1)$$

and that (b) may be written,

$$\ln q = A \left(\frac{1}{T_1} - \frac{1}{T_2} \right) \quad (2)$$

for dark body reactions. Now since $h\nu/k$ in the one, and A in the other, are expressions of energy differences, in the first case for known light absorption, in the second case for assumed black body (thermal) radiations, factor, A , in the case of chemical reactions may be replaced by $h\nu/k$; equation (2) then enables one to calculate the frequency or wave-length of the dark body reaction directly, since the energy of activation, q , may be calculated from the rates of the reaction. Among those vital processes whose light-responses are influenced by temperature, Becking shows that in many cases the calculated wave-length is in close agreement with the wave-length observed to be absorbed.

In the present paper attention will be directed especially toward those physiological processes in which no visible light is known to play a rôle directly, but whose rates of reaction are markedly influenced by temperature. In these cases it will be assumed that the energy increment is due to an increase of the mean infra-red frequency, and, therefore, that the laws for dark-body radiation hold. The phenomena investigated will be those that belong to the category of physiological stimuli as well as responses, although the latter class will receive more attention. Since all these processes go on in condensed, and often heterogeneous, sometimes suspensoid systems, doubt will be raised as to whether the laws of (infra-red) radiation actually hold, or if they appear to hold, whether any meaning could be attached to the result. For answer the reader is referred to the discussions of the physical chemists and especially to those of the champions of the radiation hypothesis of chemical reaction (3, 4).

If the energy increment, q , of a (gram-molecular) chemical reaction is due to a critical increment in radiational frequency then q should be equal to $Nh\nu$ as Einstein postulated for pure photochemical reactions, and if it is not, we may show at least what the disparity is in the two values for the physiological reactions considered. Rather than calculate the frequency according to the method of Tolman and Perrin it seems more desirable to assume the frequency to be that indicated by Wien's displacement law, and the physiological reaction to be of a dark-body radiational nature. In this case then the treatment will follow more nearly the original suggestions of Trautz, Marcellin and Haber.

II

QUANTUM RELATIONS APPLIED TO LIVING PROCESSES

1. *Respiration metabolism and photosynthesis in plants*

We take up the cases where the gram molecular heat of activation, q , of the van't Hoff-Arrhenius equation is compared with the gm. mol. quanta, $Nh\nu$. Here, as stated above, q is the energy value of the difference in maximal frequencies leading to the reaction, or the $E - E'$ difference of Haber (3). The median critical frequency concerned in the reaction is arbitrarily assumed to correspond to the median temperature, and as indicated by Wien's displacement law, $\lambda\mu \cdot T = 2882$. The inquiry then turns on the relation between $q/Nh\nu$ in all those cases where rates of reaction or response are known at different temperatures between range limits compatible with normal living matter.

In practice the equation used is in the form,

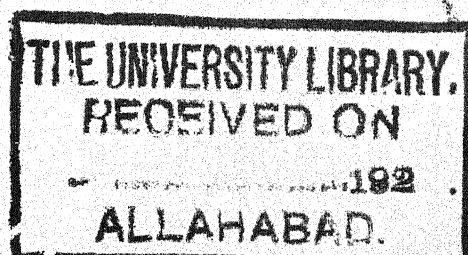
$$q = \left(\log_{10} \frac{k_2}{k_1} \right) \frac{R}{0.4343} \cdot \frac{T_1 T_2}{T_2 - T_1}$$

or, in cases where the temperature coefficient, Q_{10} , is already known,

$$q = (\log Q_{10}) \cdot 4.57 \cdot \frac{T_1(T_1 + 10)}{10},$$

of which a close approximation is to be had, when T is put median to T_1 and $T_1 + 10$, by the expression $q = 0.46 T^2 \log Q_{10}$.

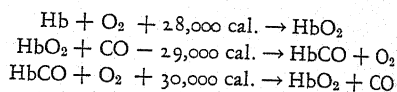
Data on plant metabolism will come first in order, since photochemical reactions in plants have been studied already from the quantum point of view, and since a fairly large body of measurements of dark-field reactions of the same proc-



absorbed; whence $q = 13,100$ and the quanta yield is 4.5 per molecule. Again the observations of Barcroft and King (5) on haemoglobin solutions when the pressure of O_2 is kept constant at 10 mm. Hg. show that 93 per cent saturation obtains at 14° and 14 per cent saturation at $38^\circ C$; whence $q = 10,370$ and the quanta yield is 3.6 per mol. at temperature 20° . Since the quanta yield as gotten from the data of Torup, Camis, Meyerhof, Barcroft and King all indicate lower values than that gotten from du Bois-Reymond's data and since the difference is roughly as 1:2:3, it would appear that we are dealing with polymeric forms of Hb.

The effect of sun light, as observed by Haldane and Smith (5), upon the reaction equilibrium, $\frac{[O_2]}{[CO]} \cdot \frac{[HbCO]}{[HbO_2]}$ arouses one's interest to an even greater extent; for the foregoing phenomena thus far have involved only the grosser thermal radiations. Hartridge and Hill (5) reported observations showing that the reduction of HbO_2 by CO was diminished not by the visible rays of the sun's light but by that portion of it represented by wave lengths lying between 850 and 1075 μ , all of which are within the infra-red. The energies of these wave-lengths, when expressed in gram-molecular quantities calculated from $Nh\nu$, lie between 33,560 and 26,580 calories, the mean of the extreme values being 30,140 calories. Now it is a striking fact that the heat of activation of the reaction $Hb + O_2 \rightarrow HbO_2$, as calculated by Barcroft and Hill (5) from their observations on rate of the reaction at 18° and $38^\circ C$, was found to be 28,000 calories, a figure corresponding to the less energetic half of the wave-lengths absorbed by haemoglobin as observed by Hartridge and Hill. If we conceive of the CO molecules in the above system as furnishing enough energy to overcome the combina-

tion HbO_2 , it probably must be something more than 28,000 calories; and in turn, if the reducing effect of the CO molecules is to be counteracted, it would be reasonable to suppose that an energy source somewhat greater than 28,000 calories would have to be available. It appears that the infra-red radiations, whose mean energy complement is 30,140 calories, are able to diminish the reducing power of CO in the $Hb + O_2 \rightarrow HbO_2$ reaction because the energy they bring to bear is just more than enough to counteract the energy of the CO molecules. One may express this triangle of mutually antagonistic forces thus:



The closeness in value of the counteracting energies may account for the fact that the reactions under ordinary conditions are never complete and that the radiations observed to be absorbed diminish the reducing power of CO on the HbO_2 compound only $1/20$ to $1/36$ of its reducing power in the presence of the longer wave-lengths. It would appear that the law of equivalence may be valid in this reaction, and only awaits experimental evidence to prove it.

This section should not be ended before mentioning certain data obtained by Gaffron (5) on chlorophyll and haematoporphyrin. When chlorophyll is dissolved in acetone and treated with light it is found that O_2 is absorbed by the chlorophyll in such quantities that the relation between O_2 and light absorbed is not only a constant but a constant approaching unity, the figures being 0.97, 1.01, 0.97, and 0.99 for red, yellow, green and blue light. Gaffron, who did this work in O. Warburg's laboratory, also showed that haematoporphyrin and other

fluorescent substances obey the law of equivalence. The quanta yield for haematoporphyrin and allylthiourea is of the order of 0.99. When acceptor is added the yield is made to deviate from 0.1 to 0.86.

Putting these remarkable facts together with the performances of chlorophyll and haemoglobin in their more normally vital activities it would seem that thermal radiations must play some important rôle in the latter that should be demonstrable by further experiments designed expressly for the purpose.

3. *Quantum relations among the obscurer physiological processes, the limits of their validity*

Having examined a few of the more obvious biochemical reactions let us now turn our attention to some of the obscurer physiological processes. Of these there are some that (it would seem *a priori*), when once revealed, will be found comparatively simple of explanation. To this group there are (1) the inner stimulus that gives rise to automatic rhythms of various sorts, (2) the true latent periods intervening between the moments of stimulation and response, and (3) the conduction of the excitatory process in muscle and nerve or indeed in protoplasm in general. It was after a consideration such as this that many of my studies on temperature coefficients have been directed toward these processes. It has been objected that temperature coefficients of such phenomena are meaningless because of the complexity of the phenomena, and that the many physical factors involved set limits to rates of reaction that in turn obscure the real rates of chemical action; finally, that the coefficients in any case hold for only a limited range. The answer to all these criticisms may some day

be given in full. Here I wish only to answer briefly.

First, there probably are no physiologists who have not thought of these limits; second, the objections offered hold even for "pure" homogeneous chemical systems, temperature coefficients always hold approximately for only limited ranges of temperature in the inorganic world.

The Arrhenius equation, $\frac{k_2}{k_1} = e^{\frac{T_2 - T_1}{T_1 T_2}}$ al-

lows for a variable temperature coefficient, and thus Q_{10} decreases between the physiological limits as the temperature increases. Finally it hardly needs to be pointed out that the temperature coefficients for expansion, and of electrical conduction for metals change as soon as solids melt or liquids congeal; the gas laws themselves have limits. It would not be strange then if temperature coefficients change when lipoids congeal at lower or liquify at the higher temperatures; when the solubilities of gases (oxygen and carbon dioxide) and viscosity of protoplasm increase inversely, diffusion rate directly, with temperature. The many studies that have appeared, in which these and others of the various physical factors involved have been investigated as to their specific rôles, are highly commendable but none of them have succeeded in changing the general proposition that in many cases, within certain ranges of temperature, the temperature coefficient is an index as to whether or not a physiological process is fundamentally of a physical or a chemical nature. And with temperature coefficient we include the Arrhenius formula; for the coefficient as well as the formula are both based upon the van't Hoff reaction isochore, the most fundamental of all formulae in chemical thermodynamics. It was with this understanding that both the heat of

activation (either as a half value, as in the term A , or as its whole value, as in the term q , or μ , in the Arrhenius formula) and temperature coefficients have been calculated in most of my papers from the very first published on the subject.

With this understanding then of the limitations imposed let us proceed to a consideration of the quanta relations of some of the simpler physiological processes of obscurer character.

4. *Quantum relations among the rhythmical processes*

It was my privilege in the years 1904-1908 to be among the first to demonstrate that certain of the unexplained physiological processes, in their rates of reaction as influenced by temperature, obey the rule of van't Hoff-Arrhenius, within certain limits and behave, therefore, like purely chemical systems. In a summary of some fifty such cases (6, 1908) it was pointed out that the heat constants in the Arrhenius equation tend to be of the same ranges of magnitude as had been found for many chemical reactions, that there is a tendency for the values to be the same for physiological processes of like character, and finally that there is a suggestion that the heat values (expressed there as $\mu/1000$) fall into multiples of four. (See the last column in the tables on pp. 330-333 of my 1908 paper on "A Comparative Study of Temperature Coefficients," cited above.) At the time I had no explanation to offer for this tendency and so did not discuss the point. In the light of the quantum theory, however, there seems to be some possible explanation. One's curiosity concerning the cases brought together in that initial list will be satisfied on this point perhaps when I say that of 17 of the more reliable observations on the spontaneous rhythms of muscular organs the quanta yields vary from 4.0

to 6.9 with a mean value of 5.5, and that only eight out of the 17 yield figures for quanta that are nearly whole numbers. The eight cases yield quanta of 6.08, 4.05, 6.91, 5.08, 5.00, 4.13, 6.02 and 6.12. It is thus clear thus far that one can attach no significance to their whole-number character.

Of the later studies on rhythmic processes there are three different groups that may be recalled with profit. First there is the series of experiments on the isolated mammalian heart that I carried through with the aid of two of my students, Messrs Elmdorf and Fallas (6, 1913). In one case a dog's heart beat for hours at very widely different temperatures; the plotted rates fall about a logarithmic curve the extreme points of which give a rate of 35.2 at 23.5° and 116 at 40.4°C. The heat of activation, q , in this case equals 13,270 and the ratio $q/Nh\nu$ at 32° yields 4.43 quanta. In the same series a cat's heart beat with rate of 18.5 at 20° and 122 at 40°C, whence $q = 17,400$ and $q/Nh\nu$ (with thermal frequency taken for 30°C) gives 5.85 quanta. A second study is one on the flashing interval of fire-flies (6, 1920). The observations were made on successive evenings during one summer and thus at various temperatures. At 28.55° the rate of flash was found to be 15.2 times per minute; at 19.4°, 8.1 times per minute. Whence one calculates 4.13 quanta at 24°C per molecule of the stuff that sets off the nervous reflex producing the flash in the fire-fly.

Locomotion in animals is a sort of rhythmical activity and after once started is maintained doubtless with comparatively simple mechanism so long as no complicating factors intervene. For a discussion of this point see my paper of 1904 (6). A number of researches have been published on the influence of temperature on the rate of locomotion. For

our third type of rhythmicity however I take the results of only one of the more recent studies, that of Shapley (6). This observer finds evidence of an abrupt change from one value to another of the temperature coefficient for 10-degrees interval and argues that if two reactions (among the many involved) limit and control the resultant temperature coefficients, then the μ ($\equiv q$) values may be indices of this. This author finds for the species of ant, *Liometopum*, $Q_{10} = 3.3$ at the median temperature, $T_m = 288^\circ$ abs., and $\mu = 19,800$; with $Q_{10} = 1.9$, $T_m = 302^\circ$ abs., $\mu = 11,700$. At these two values of T_m , $Nh\nu = 2833$ and 2965 calories respectively whence the quanta yield at the two energy levels become $19800/2833$ and $11700/2965$, or 6.99 and 3.94 respectively, both figures being whole numbers within 1.5 per cent as extreme variations.

As a final example of rhythmicity I take one from the inorganic world, the phenomenon of rhythmicity in passive iron as observed by R. S. Lillie (6). After once setting up a wave of activation on a suitable ring of passive iron wire the activity is maintained by the first wave automatically giving rise to another indefinitely. The rate of rhythm at 10° is about 15, at 30° about 125 per minute, representing a q -value of 18,190 calories and a quantum yield at the median temperature of nearly 6.3 per molecule, or ion, of the substance responsible for the rhythmical oxidation-reduction phenomenon.

5. Quantum relations in the processes of conduction of the excitatory state

Let us now pass on to a consideration of the phenomenon of conduction. As data I shall take the results of my study of the influence of temperature upon the velocity of impulse in frogs' motor nerves (7). In the accompanying figure the

curve connects the statistical means of the observations at temperatures about five degrees apart. The interrupted line, continuing the curve a distance for the higher range of temperature, represents the velocity of conduction in mammalian motor nerve as observed by Professors Erlanger and Gasser and their associates (7), and is added only as giving evidence that the nature of motor nerve in both classes of

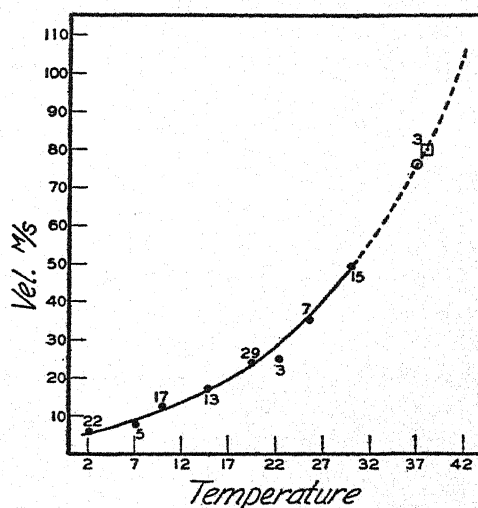


FIG. 1. MEAN VELOCITIES OF CONDUCTION AT VARIOUS CORRESPONDING MEAN TEMPERATURES

Those for frog's sciatic nerves are shown by the symbols, •••••, and represent 111 observations on nerves from 12 different fall frogs (Snyder, 1908). The symbol ○ is the observation of Felix (1923) on the motor-sensory nerve-trunk in the leg of man. The symbol □ is the mean of three determinations by Erlanger and Gasser (1924) on the dog's tibial nerve. The numerals attached to the symbols indicate in each case the frequency of the observation.

vertebrates is probably very much the same.

In the following table I have assembled the various values that may be calculated from these data, taking points exactly five degrees apart on the smoothed curve. The symbols in the first column stand for velocity of conduction in meters per second, M/Sec.; temperature coefficients for intervals of ten degrees, Q_{10} ; heat of

activation in calories as calculated from the Arrhenius equation, q ; the assumed effective radiation wave-length in thousandths of a mm. for each temperature as determined by Wien's displacement law, $\lambda\mu = 2882/T$; and finally the quanta yield per molecule of the hypothetical substance primarily involved in the probable physico-chemical reaction, $q/Nh\nu$.

From table 2 it is seen that these mean values of Q_{10} , q and quanta are all pretty constant between, say, 15° and 35°C for frog motor nerve, and that they have the same magnitudes for the few observations on mammalian motor nerves. Below 15° , however, all the terms increase more

yield appears to be the more significant, the average of the mean values for the temperature range above 12° being 4.16, whereas the value for the range from 2° to 12° is 5.18, a gain of a whole quantum.

But there may be objection to assuming the wave-length to be that corresponding to the prevailing temperature; it may be assumed rather that the law of equivalence holds, in which case $q = Nh\nu$, and (since q , N and h are known) that the radiation frequency should rather be calculated from this latter equation. In this case the effective wave-length turns out to be $1/5$ and $1/4$ less than those assumed in the table above, that is, $\lambda\mu =$

TABLE 2
Quantum relations in rate of motor nerve conduction

Temperature, deg. C.	OF FROGS' SCIATIC NERVES						OF DOG'S SKELETAL MOTOR NERVES		MEAN BE-TWEEN 12° AND 42°	MEAN BE-TWEEN 12° AND 32°
	2	7	12	17	22	27	32	37	42	
Conduction, M/Sec.	5.7	8.8	13.6	19.7	27.8	40	56	76	106	
Temperature coef., Q_{10}		2.38	2.24	2.02	2.07	2.07	1.90	1.89		1.99
q , in calories.		14,260	12,970	12,200	12,250	12,480	11,880	12,430		12,248
$\lambda\mu = 2882/T$	10.4	10.25	10.10	9.93	9.77	9.60	9.45	9.30	9.16	
$q/Nh\nu = \text{quanta}$		5.18	4.63	4.28	4.24	4.24	3.97	4.08		4.16

or less abruptly so that between 2° and 12° they have values markedly greater than any variations in their values between 12° and 42° ; the increase being in round numbers 10 per cent for Q_{10} , 16 per cent for q , 25 per cent for the quanta yield. This more or less abrupt change in the q value is what Crozier (7) has referred to as a change in "temperature characteristic," or in "critical increment," a term he uses "to provide a name for the E or μ in the van't Hoff-Arrhenius equation, which should be free from the connotation of any particular view as to the mechanism of activation." But, as the reader sees, the increase in quanta

2 and somewhat > 2 . These are still in the infra-red but correspond to temperatures much higher than the observed. Now such radiation frequencies are not impossible any more than the still higher ones that are absorbed in the "cold" photochemical reactions. Nevertheless since the frequencies in the latter correspond beyond doubt to those portions of the spectrum that are known to be absorbed, whereas the only known radiations concerned in nerve processes are those corresponding to the observed temperatures, we must believe, until contrary proof is adduced, that the longer wave-lengths given in the table above are

more probably the ones absorbed. This latter conclusion is supported further when we recall that even in photochemical reaction of the green plant as observed by Warburg and Negelein (see above), the quanta yield did not turn out to follow the law of equivalence, but had the values 5 and 4, values nearly the same as we here find to be true for nerve conduction from its thermo-chemical reaction.

From the observations of R. S. Lillie (7) on the influence of temperature on rate of conduction of the activation wave in "passive" iron wire the quantum yield appears to be of a similar order.

6. Summary of the findings of Chapter II

In table 3 I have summarized the quantum yield thus far revealed by this analysis of various physiological processes.

TABLE 3
Summary of mean ratios of thermal quanta and number of molecules acting

OBSERVER	ACTIVITY	$q/Nh\nu$
Kuijper, 1910.....	CO ₂ given off by seedlings	5.67
Yabusoe, 1924.....	O ₂ used up by chlorella	3.99
Matthaei, 1904.....	CO ₂ absorbed by green leaf	4.0
Osterhout and Haas, 1919.....	CO ₂ absorbed by green alga	3.6
Warburg, Q., 1919.....	ditto, light intensity = 16	8.8
		4.0
	ditto, light intensity = 45	8.2
		4.34
R. du Bois Reymond, 1914.....	Oxidation haemoglobin	2.88
Torup, 1906.....	ditto	7.85
Barcroft and King, 1909.....	ditto	3.92
Barcroft and Hill, 1910.....	ditto	3.6
Camis, 1907.....	Oxidation of defibrinated blood	9.96
Meyerhof, 1912.....	Oxidation erythrocytes	3.54
Snyder, <i>et al.</i> 1908.....	Muscular rhythmical contractions, 17 experiments, extremes	4.5
Snyder, <i>et al.</i> , 1913.....	Rate of heart beat, dog's cat's	4.0
		6.9
Snyder, <i>et al.</i> , 1919.....	Flashing interval, fire-flies	4.43
		5.85
Shapley, 1924.....	Rate of locomotion in ants, 1925	4.15
		6.99
Lillie, R. S., 1928.....	Rhythmicity in passive iron	3.94
Snyder, 1908.....	Rate of conductivity in motor nerves	6.3
		4.16
Rosenberg and Sugimoto, 1925.....	ditto	5.18
		4.27

In passing it may be pointed out that the researches of Tanaki (7) and of Rosenberg and Sugimoto (7) working in Professor Cremer's laboratory have disposed of the doubt raised by Broemser (7) concerning the reality of temperature affecting conduction rate in nerve. The results of Rosenberg and Sugimoto indicate a similar quantum yield, namely 4.27.

It will be noted that the numerical values approach whole numbers within ± 20 per cent in 17 out of the 26 cases and that they all appear to lie within the limits of 3 to 10 quanta. If one refers to the summaries of quanta yields thus far determined for purely photo-chemical reactions, for example in Kistiakowsky's book (1), one finds that the results show much greater

deviation than obtains here among this group of physiological actions. Of course it should be remembered that all thermal chemical reactions, with temperature coefficients lying between 2 and 3, theoretically should give quanta yields of the order found in this table.

III

QUANTUM RELATIONS IN MUSCLE METABOLISM

In the foregoing chapter we have assumed that the q value of the thermodynamical equation expressing rate of chemical reaction is approximately a correct measure of the effective energy exchange in the reaction. In doing so we have relied upon observations of temperature and rates of reaction of the physiological processes as being all sufficient data for the determinations of the energy exchange, and, provisionally, therefore, of the radiation assumed to be absorbed or emitted. In the second section of Chapter II a few cases are given where both energy as well as amount of substance reacting are known in certain biochemical processes (absorption of O_2 by Hb). In the present chapter I wish to take up a few cases of the more complex processes in which both the energy and the material exchanges have been more or less completely measured, if not in one and the same experiment, at least in different experiments upon similar tissues and organs.

1. *The observed heat production and gaseous and carbohydrate metabolism of contracting cardiac muscle*

The heat produced in automatically beating heart has been a subject of frequent observation. The difficulty with this muscle as with smooth muscle has been to produce complete anaerobiosis.

Experiments are now under way where (as more fully treated of below) the method applied to smooth muscle (8) is being applied also to the heart muscle. Until these redeterminations are complete we shall have to content ourselves with the earlier data and allow for the probable difference.

There seem to be few researches in the literature on the chemical changes going on in the beating turtle heart. On the other hand there is an embarrassing abundance of material in the literature on oxygen and carbohydrate metabolism of frog and mammalian hearts. When one surveys the results of these investigations and tries to reduce them to a common standard of comparison the task is almost hopeless. The problem is to find out from the data the quantity of oxygen used by unit mass of muscle per beat and per unit tension developed during that beat. Most of the data given are per unit weight of muscle per hour; often either the rate, or the exact temperature, is not given, nor is it always clear whether the volume given has been reduced to standard condition of pressure and temperature. The factor of tension, as I finally chose it, is the one in greatest doubt; in one or two cases it may be 200 per cent removed from the true value. When no data were given by the author from which tension could be calculated, I assumed 1 gm. muscle exerted 30 gm. tension. Bohnenkamp, Eismayer and Ernst (13) on the basis of their recent observations have concluded that tension has no influence on oxygen consumption of the heart, that organ being in this respect, as it is in others, all-or-none. However, this does not appear to be borne out by the work of Rohde and others and, until established by further investigation, cannot be accepted. In the table below the results of various observers have been reduced to a standard common to all,

that is, to the volume in cc. of oxygen used by 1 gm. muscle per beat and per 1 gm. maximum tension exerted during the beat. For the literature see note (13).

The oxygen used per gm. muscle per gram tension per beat by various kinds of hearts, in cc. $\times 10^{-6}$

Tortoise heart, Vernon (1910, CO ₂ output observed; assuming R.Q. = 1).....	3.7
Frog heart, Weizäcker (1912).....	18.7
Lüscher (1920, 48.3; 1921, 38.7).....	43.3
Bohnenkamp, <i>et alia</i> s (1928).....	33.0
Mammalian heart, Barcroft and Dixon (1907).....	4.0
Rohde (1912).....	17.0
Starling and Evans (1914).....	14.6

With these it is interesting to compare the data for skeletal muscle in cc. O₂ $\times 10^{-6}$:

Sartorius of frog, Fenn (1928, 1 exp't. only).....	7.1
Gastrocnemius, frog, Parnas (1921).....	4.5
Meyerhof and Schulz (1927).....	4.3

The mean for the seven researches on heart is $11.6 \cdot 10^{-6}$ cc. of oxygen. It is surprising to find that skeletal muscle uses less than half as much oxygen. As will be shown below, smooth muscle when its O₂ consumption is reduced to a similar basis appears to use $200 \cdot 10^{-6}$ cc., a figure nearly forty times more than that for gastrocnemius and nearly seventeen times more than that for heart muscle. An inaccurate tension factor could not be the cause of such great deviations. For if I allow 60 gram tension per gm. smooth muscle instead of 30, the O₂ used would still be nearly twenty times that used by gastrocnemius muscle.

The studies on carbohydrate metabolism in various mammalian heart muscles show no such great deviations. (For the literature see note 13.) Put in terms of gram carbohydrate used up per gm. muscle per gm. maximum tension exerted, I find the following (The figures in each case should be divided by 10^8):

Mammalian heart,—cat, Müller, 1904.....	0.88
rabbit, Locke and	
Rosenheim (1907)...	0.43
cat, Rohde (1910).....	1.00
dog, Knowlton and	
Starling (1912).....	1.23
rabbit, Underhill and	
Prince (1914).....	0.83
Mean of 5 investigations.....	0.87

Knowing now the ranges in the amounts of carbohydrate used up by mammalian heart muscle, one may calculate the O₂ required and compare the calculated with the observed quantities. This will be $0.87 \cdot 10^{-8} \cdot 1.92/180 = 0.93 \cdot 10^{-8}$ gm., or $6.5 \cdot 10^{-6}$ cc. of oxygen required, a number that is nearer the quantities observed for frogs' leg muscles and the two smallest observed quantities on heart muscle (*v. supra*) and is only a little more than one half of the mean value of all seven observed quantities of oxygen used by heart muscle.

The quantity of carbohydrate mobilized during contraction, while pretty well established for skeletal, has not been observed at all, to my knowledge, for cardiac muscle. One can only indirectly calculate the amount, and to do so may set out from the oxidation quotients known for skeletal, and as shown for smooth muscle when allowed to rest first in oxygen-want and then in oxygen-plenty. The quotient for smooth muscle as given by Evans (10) is 1/3.55. In studies on carbohydrate metabolism of frogs' gastrocnemius muscle Parnas (16) put the quotient at 1/4.0; Meyerhof and Schulz (12) at 1/4.7. (I calculate that the total carbohydrate mobilized by gastrocnemius muscle as observed by the former was $2.3 \cdot 10^{-8}$ gm.; as observed by the latter, $2.68 \cdot 10^{-8}$ gm. per gm. muscle and gm. tension.) The observed carbohydrate oxidized by heart muscle multiplied by the known oxidative quotients for different muscles then gives the quantities $2.92 \cdot 10^{-8}$, $3.49 \cdot 10^{-8}$ and $4.9 \cdot 10^{-8}$ gm.

respectively as possible quantities of carbohydrate mobilized during the systole. Let us assume that the middle figure, corresponding to Parnas' quotient $1/4$, is the more nearly correct one. It may be stated then tentatively that during the beat there are $6.5 \cdot 10^{-6}$ cc., $0.093 \cdot 10^{-8}$ gm., oxygen used and $3.49 \cdot 10^{-8}$ gm. carbohydrate mobilized. These numbers when multiplied by the Avogadro constant give $17.6 \cdot 10^{13}$ molecules oxygen, and $11.7 \cdot 10^{13}$ molecules carbohydrate respectively.

As will be shown later the anaërobic heat production as observed in the heart will require some correction. On page 86 of my paper (11) the total anoxidative heat is given as $3.2 \cdot 10^{-5}$ cal. For this I shall now subtract $1/5$ which I believe is a fair estimate of the still uncorrected heat of oxidative origin. The proper oxidative heat given as the observed amount thus will be increased somewhat; in addition one must add the heat that is probably absorbed by synthesis of lactic acid into soluble glycogen. The revised figures are as follows in terms of microcalories:

Total "anoxidative" h.p. observed, 1928	32
$1/5$ to be deducted for O_2 leaks	6
Corrected total anoxidative h.p. observed	26
Total heat observed in oxygen, 1928	79
Corrected anoxidative heat	26
Corrected oxidative heat observed	53
Absorbed heat due to synthesis	15
Total heat of oxidative origin	68
Total heat produced per heart beat	94

The amount to be added as the heat absorbed during the resynthesis of carbohydrate is calculated from the oxidative quotient, $\frac{1}{2}$, and the carbohydrate mobilized. The amount synthesized theoretically being $\frac{3}{4}$ of the amount mobilized, we have $0.75 \cdot 87 \cdot 10^{-8}$ or $6.53 \cdot 10^{-8}$ gm., the heat equivalent of which must be $6.53 \cdot 10^{-8}$ ($3836 - 3601$) = $15.3 \cdot 10^{-8}$ cal.

Lundsgaard (Biochem. Zeit., 1930, 217: 162) has just shown that muscle poisoned with mono-iodo-acetic acid is able to contract anaerobically without the production of lactic acid. Since E. Fischer (Die Naturwissenschaften, 1930, 18ter Jahrg. 736) has shown that the ratio of heat production to tension in anaerobic muscle poisoned with brom-acetic acid remains the same as has been found for normal anaërobic muscle, it would seem that some substance or substances other than lactic acid, but of equal calorific value are formed under the influence of the iodo- or Br-acetic acid. Lundsgaard has shown that the source of energy is probably in the breakdown of phosphogen.

The values put in terms of quanta are $26 \cdot 10^{-6} \cdot 4.19 \cdot 10^7 / 18.65 \cdot 10^{-14}$, or $5.85 \cdot 10^{14}$ quanta of anoxidative heat, and $68 \cdot 10^{-6} \cdot 4.19 \cdot 10^7 / 19.23 \cdot 10^{-14}$, or $14.8 \cdot 10^{15}$ quanta of oxidative heat.

Comparing with molecules in each case, the quanta yield is $585/11.7$, or about 50 quanta per molecule of carbohydrate mobilized, and $148/17.6$, or about 8 quanta per molecule of oxygen used, during the heart beat. If, instead of $6.5 \cdot 10^{-6}$ cc. oxygen as the observed volume used, we take the highest amount observed, namely $48.3 \cdot 10^{-6}$ cc. (Lüscher, on frog, 1920), then the ratio becomes 1.08 quantum per molecule of oxygen; if the carbohydrate mobilized is the chemical equivalent of this amount of oxygen times the denominator of the $1/4.7$ oxidation quotient, then the number of molecules mobilized is $10.2 \cdot 10^{14}$ and the quanta yield is $58.5/10.2$ or 5.8 quanta of anoxidative heat for each molecule of carbohydrate.

In other words only if one utilizes selected data on heart metabolism instead of the average of all data, does one find the law of equivalence valid for the oxidation process and the quanta yield for carbohy-

drate metabolism very similar to that for most other physiological processes (as exhibited in table 3).

2. *The observed heat production and metabolic exchanges of contracting skeletal muscle*

Passing on to skeletal muscle I may start with the initial heat production of frog's gastrocnemius muscle as observed by Snyder and Gemmill, 1925 (14). The mean of 31 observations on 6 different pairs of muscles stimulated through their nerves is $2.87 \cdot 10^{-5}$ calorie, the mean for the six different pairs irrespective of the number of observations on each pair is $2.83 \cdot 10^{-5}$ calorie. The mean temperature of these muscles was 8.32°C . The initial phase of heat production of the leg muscle of the frog is of comparatively very short duration and it is hard to imagine, even though enough oxygen is present, how oxidation could have time enough to add to the initial heat. However, when one recalls that silver atoms have been observed to orient themselves completely in a magnetic field in the brief period of 10^{-4} second (Stern and Gerlach) and that the time of exposure in the electric-spark photograph is no longer than one half millionth of a second, it would seem that a good deal of carbohydrate may combine with O_2 in say 0.1 of a second if the molecules are near each other at the outset. Moreover, in view of the great difference in initial heat observed in smooth muscle, —a difference of 66 per cent, when in .01 per cent oxygen compared with that when in .001 per cent oxygen (8), it will not be excessive in my opinion if we deduct one-third from the observed initial heat in gastrocnemius muscle, when in oxygen plenty, to get at the real anoxidative heat. This then will be $2.87 - 0.92$, or $1.95 \cdot 10^{-5}$ cal. The total observed heat production of unfatigued sartorius muscle in oxygen according to the latest revision by

A. V. Hill (15) is 2.07 times the anaërobic heat. The ratio for gastrocnemius doubtless is the same and we may, therefore, conclude that the total heat production of this muscle is 2.07×1.95 , or $4.04 \cdot 10^{-5}$ cal. The observable oxidative heat then is $4.04 - 1.95$, or $2.09 \cdot 10^{-5}$ cal. As shown above to this observable oxidative heat we must add the amount absorbed during the resynthesis of 3.7/4.7 of the mobilized carbohydrates, which is $2.68 \cdot 10^{-8} \times 3.7/4.7$ ($3836-3601$) = $0.45 \cdot 10^{-5}$ cal. The total heat of oxidative origin then is $2.09 + 0.45$, or $2.54 \cdot 10^{-5}$ cal.

The mean temperature of the gastrocnemius muscles was 8.32°C ; $h\nu$, therefore, equals $19.1 \cdot 10^{-14}$ ergs. From this the heats as determined are: for the *anoxidative phase*, $1.95 \cdot 10^{-5} \cdot 4.19 \cdot 10^7 / 19.1 \cdot 10^{-14}$, or $4.28 \cdot 10^{15}$ quanta; for the *oxidative phase*, $2.54 \cdot 10^{-5} \cdot 4.19 \cdot 10^7 / 19.1 \cdot 10^{-14}$, or $5.56 \cdot 10^{15}$ quanta.

The carbohydrate mobilized by frog gastrocnemius muscle as determined by Meyerhof and Schulz (12, p. 568) is $2.68 \cdot 10^{-8}$ gm. per gm. muscle and gm. tension, if one divides their figures given in column 4, of Table 3 section C, by the corresponding tensions of the "a" muscles. The authors conclude that 1/4.7 of this carbohydrate was oxidized. The actual oxygen used by the muscles is also given by the authors, but for our purpose we may rely upon calculating back from the oxidation quotient. Thus there are $2.68 \cdot 10^{-8} \cdot 6.06 \cdot 10^{23} / 180$, or $0.9 \cdot 10^{14}$ molecules of carbohydrate mobilized; there being 6 O_2 molecules required for each molecule carbohydrate burned there will be then $6 \cdot 0.9 \cdot 10^{14} / 4.7$, or $1.15 \cdot 10^{14}$ molecules of oxygen. The quantum yield in each of these cases is: $4.28 \cdot 10^{15} / .09 \cdot 10^{15}$, or 47 quanta per molecule of carbohydrate mobilized and $5.56 \cdot 10^{15} / .12 \cdot 10^{15}$, or 49 quanta per molecule of oxygen used by the muscle.

For sartorius muscle of frog one may

start out from the data given by Hill and Hartree (1922) who observed the mean initial heat to be .0074 gm. cal. In view of the great avidity for oxygen that muscles show (8) we may subtract $1/3$ from this number also and put .0074 - .0024, or .005 cal. as the initial heat of 1 gm. muscle. The tension exerted by 1 gm. of these sartorius muscles I find to have been 292 gm., hence the initial heat becomes $1.7 \cdot 10^{-5}$ cal. per gm. tension. The total heat (using the 2.07 ratio again) becomes $3.54 \cdot 10^{-5}$, and hence the observable oxidative heat $3.54 - 1.70$ or $1.84 \cdot 10^{-5}$ cal. Adding to this the heat absorbed by synthesis we have $1.84 + 0.45$, or $2.29 \cdot 10^{-5}$ as the total oxidative heat. These heats in terms of quanta (putting $h\nu$ at 1.5°C . *ca* the temperature of the observations) are $3.85 \cdot 10^{15}$ quanta of anoxidative heat and $5.14 \cdot 10^{15}$ quanta of oxidative heat, figures not greatly different from what were found above for the gastrocnemius muscle. Since the number of molecules engaged in sartorius contraction will have to be calculated from the same data used above for gastrocnemius the quantum yield will be only a little less, namely about 41 and 43 quanta for the two heats respectively. On the other hand while the order of magnitude of quanta for the anoxidative phase is the same for both cardiac and skeletal muscle, it possibly differs for the oxidative phase of contraction, the quantum yield there just possibly obeying the equivalence law in the case at least of heart muscle.

3. *The observed heat production and metabolic exchange of contracting smooth muscle*

In a recent study of heat production of smooth muscle (8) it was shown that the total heat due to oxidation, per gram weight of muscle per gram tension exerted per contraction, has a value of $32 \cdot 10^{-6}$ calorie ($27.5 + 4.5 \cdot 10^{-6}$) for muscles in balanced breathing in an excess of oxygen.

In the presence of an atmosphere containing less than .001 per cent oxygen the same muscles produced a total "anoxidative" heat of $11.6 \cdot 10^{-6}$ calorie. Again let us regard these heats as measures of effective radiant energies involved in the reactions. Then their quantities reduced to ergs and divided by the appropriate value of $h\nu$ will give the quanta required in each. The mean temperature of the experiments was 20.5°C with extreme variations $\pm 1.8^\circ\text{C}$ through the series. We, therefore, put $h\nu = 20 \cdot 10^{-14}$. The oxidative process in the muscle contraction thus has a value of $\frac{32.44 \cdot 10^{-6} \cdot 4.19 \cdot 10^7}{20 \cdot 10^{-14}}$,

or $6.6 \cdot 10^{15}$ quanta, and the anoxidative process a value of $11.6 \cdot 10^{-6} \cdot 4.19 \cdot 10^7 / 20 \cdot 10^{-14}$, or $2.43 \cdot 10^{15}$ quanta.

From our knowledge of the chemistry of isolated muscle during activity there is almost conclusive evidence that not only skeletal but also smooth muscle in survival experiments oxidizes carbohydrate almost exclusively during the oxidative process. During the anoxidative process there is still much doubt as to what chemical changes go on, but whatever they are, the mobilization of carbohydrate into a substance of a calorific value equal to that of lactic acid seems to be by far the chief reaction, and, as was made probable in the paper just cited (8), may be the cause of the whole of the so-called anoxidative heat production. (Compare p. 294.)

No measurements of oxygen used or carbohydrate metabolism were made directly in the smooth muscles during the observations of heat production. Such determinations, however, have been made by others on smooth muscle as well as upon skeletal, and while it may seem far-fetched to compare quantitatively results from other workers under somewhat different conditions, nevertheless the striking similarity I have found in the quantity of

heat produced by quite different smooth muscles when reduced to a common standard of comparison leaves little doubt that simultaneous direct metabolism determinations will likewise lead to a very similar result wherever done or upon whatever smooth muscle one chooses to study. For oxygen consumption we have the results of C. L. Evans (9, 1923) which, when reduced to a basis of 1 gm. muscle per hour I make out to be about 0.12 cc. at 20°C. Taking 30 gm. as the mean tension exerted in the contractions (10), we may say these smooth muscles used in three-minute periods (the probable time of a rhythmical contraction) $0.12 \cdot 3 / 60 = 30$, or $2 \cdot 10^{-4}$ cc. per gm. muscle per gm. tension per contraction, which is equal to $2 \cdot 10^{-4} \cdot 1.429 \cdot 10^{-3} \cdot 6.06 \cdot 10^{23} / 32 = 5.4 \cdot 10^{15}$ molecules of oxygen.

The energy of the anoxidative processes of smooth muscle contraction, we may assume, comes from the breakdown of carbohydrate into lactic acid, direct evidence for which is given by Evans (10), who further concludes (p. 389) that 1/3.35 part of the lactic acid formed during the muscle action is oxidized completely while the rest, as in skeletal muscle, is resynthesized back to glycogen. The oxygen consumed in the smooth muscle action being already given, one may calculate back to the total amount of soluble carbohydrate probably mobilized in the reaction, that is, following the physiological stimulus. Thus, since six molecules of oxygen are required in oxidizing one molecule of carbohydrate, we have the ratio $6:1::5.4 \cdot 10^{15}:X$. Since the ratio of oxidized to mobilized is 1/3.35, then $3.35X = 3.0 \cdot 10^{15}$ molecules, the total mobilized carbohydrate. As shown above there were $2.43 \cdot 10^{15}$ quanta of heat liberated in the anoxidative process. *The ratio of molecules to quanta*, therefore, is $3.0 \cdot 10^{15} / 2.43 \cdot 10^{15}$, the quotient of which is

1.24. It would seem that the number of molecules to the quanta of heat engaged in the chief reaction of the anoxidative phase of smooth muscle contraction is not far from unity.

It was shown that the number of molecules of oxygen required in the oxidative process is $5.4 \cdot 10^{15}$ and the corresponding oxidative heat quanta, $6.6 \cdot 10^{15}$. The ratio of molecules of oxygen to quanta thus is $5.4/6.6$, the quotient of which is 0.82. If the molecules of carbohydrate and oxygen are added together and their total number divided by the sum of anoxidative and oxidative quanta then we have a ratio of $8.4/9.03$, or 0.93 molecules of both kinds per quantum of heat.

4. *The value of the effective frequency as calculated from the observed data on smooth muscle and as demanded by Wien's law of displacement and Einstein's law of equivalence*

Another way of comparing our experimental data with the radiation hypothesis of energy exchanges, as stated in the introduction of this essay, is to apply Wien's law of displacement directly. Let us assume that the data indicate that the equation for equivalence holds for the process of smooth muscle contraction, that is $q/Nh = 1$. Then it follows that $\nu = q/Nh$, where the sum of the mean heats observed for oxidative and anoxidative phases, namely $43.6 \cdot 10^{-6}$ calorie, may be substituted for q in terms of ergs, and the sum of the mean number of oxygen molecules and molecules of carbohydrate mobilized may be substituted for N , namely $8.14 \cdot 10^{15}$ molecules. Then,

$$\nu = \frac{43.6 \cdot 10^{-6} \cdot 4.19 \cdot 10^7}{8.4 \cdot 10^{15} \cdot 6.55 \cdot 10^{-27}} = 3.3 \cdot 10^{13}$$

which is the frequency of the effective radiant energy. Since the frequency is a function of the wave length, and since according to Wien's law, $\lambda \mu T = 2882$, we

are able to calculate the mean temperature at which the muscles functioned. For it is obvious that given $\lambda = C/\nu$, Wien's equation may be written, $T = 2882\nu/C$. In solving for T the velocity of light, C , is put in terms of $\mu/\text{sec.}$ and the frequency of the effective radiant energy found above is substituted for ν ; whence $T = 2882 \cdot 3.33 \cdot 10^{13} / (3 \cdot 10^{14}) = 319.9$ degrees absolute. Now the mean temperature of the smooth muscles in the heat-production determinations, as stated above, was $20.5^\circ\text{C} \pm 1.8$. In terms of the absolute scale this is $273.2 + 20.5$, or 293.7 degrees, a figure that is 8.2 percent less than the figure required by theory, but even so in much closer agreement than usually obtains among physiological processes.

5. *Summary and discussion of the findings of Chapter III*

Summing up the results of the inquiry thus far made on muscle in balanced breathing and in a unit of physiological action, we may say, on the radiation hypothesis of chemical activation, that (a) For smooth muscle about 1.2 molecule of carbohydrate appears to be mobilized per quantum of observed anoxidative heat, and about 0.8 molecule of oxygen is used per quantum of observed oxidative heat; or that about 0.93 molecule of the total carbohydrate and oxygen is engaged per quantum of the total observed heat production. (b) For heart muscle it may be that from 6 to 50 quanta of heat energy are required per molecule of carbohydrate mobilized, and from 1 to 8 quanta per molecule of oxygen used. (c) For skeletal muscle in a complete contraction-recovery from 41 to 47 quanta of anoxidative heat appear per molecule of carbohydrate mobilized and from 43 to 49 quanta per molecule of oxygen used.

The close agreement, in the case of smooth muscle, with the law of equivalence,

however remarkable, can not as yet be considered established. For the data upon which the calculations are based as to oxygen and carbohydrate metabolism are all too meagre. Nor may we hope that additional metabolism investigations of the kind that have been lavished upon heart muscle in the past, if once directed toward smooth muscle, will lead to more certain conclusions. As for the heart muscle, although one or two observations meet the demands of the law of equivalence, many others do not. The discrepancy seems to lie among the observations of the chemical changes, the amount of carbohydrate mobilized not having been observed at all. The observations of carbohydrate and oxygen used by the heart vary greatly even after reducing them to a common basis of comparison. The lower quanta-yields for the heart muscle are more nearly equal to the quanta-yield found for many other physiological processes. The great divergence of observations in heart muscle appears to be due in large part also to lack of uniformity of experimental conditions, and the want of a common standard for measurement. To measure the chemical changes occurring in hearts during unit time has no sense whatever. A unit of physiological response should be made the basis; at least the number of these units should be observed along with the time units.

As for the observations on skeletal muscle, it would seem that the above criticism would not apply so justly. In recent years much accurate work has been done on these muscles, the unit of physiological response being kept well in mind. But it is just here that quanta yield also indicates that the law of equivalence does not apply. Whether later it can be shown that the law holds for the primary reaction, and just what that

primary reaction may be, cannot now be stated. In passing it may be pointed out that the quanta relations in skeletal muscle remind one of the finding of E. Newton Harvey (2) in his work on the luminiferous material extracted from the crustacean, *Cypridina*. Only the quantum yield here appears to be just the reverse; instead of an excess of quanta Harvey finds an excess of molecules, at least 50 molecules of oxygen being required for each quantum of light emitted by the luciferin + O₂ reaction.

IV

RELATION OF ENERGY AND IONIC EXCHANGES IN PHYSIOLOGICAL STIMULATION

Physiological stimulation has already been considered in part in the chapter dealing with rhythmical processes. For the rate of spontaneous rhythms, within limits, *is determined by the rate of development of the inner stimuli*. As we have seen (see the summary, p. 291) the $q/Nh\nu$ value of the processes examined lies between 4 and 7. In this chapter it is proposed to deal briefly with external stimuli, inadequate and adequate, that may be applied to nerve and sense organs.

Whenever the energy of the effective stimulus can be measured then the relation between that energy in terms of quanta and its effect in terms of the number of molecules or ions made reactive may be estimated. Indeed, whatever the outcome of such a study may be, one positive result should be gained, namely, a more definite idea as to the relative number of molecules or ions probably made reactive at the point of the effective stimulus and hence the number necessary to set up a nervous impulse.

The difficulty of making a correct estimate of quantum relations and stimulating intensities appears at once when one considers that most stimuli fall on indiffer-

ent tissues as well as the particular tissue one wishes to stimulate. Electrical currents applied to nerve-trunks must traverse intervening connective tissue, myelin sheaths, intercellular fluid, etc., before reaching the axons; all of whose resistances, and, therefore, whose share of current, we have little chance of knowing. For the same reason adequate stimuli are difficult to evaluate quantitatively. In selecting data from the literature, therefore, care must be taken to select only those where excess energy as well as the loss of exciting energy has been taken into account. Let us begin with a consideration of stimulations that are quite obviously of the radiational type.

1. *The probable number of molecules or ions made reactive by a least effective electrical stimulus*

We may begin with an example of artificial or inadequate stimulation, the commonly used electrical stimulus. This has all the objections just mentioned. A strength of current equal to that of the natural bioelectric current is known to be intensive enough to act as a stimulus to other tissue, as is exemplified in the classical rheoscopic frog. Among the estimates of the absolute value of the energy exchange in the passage of an action current we have those of A. V. Hill (17). Basing his calculation upon the observed E.M.F. and duration of the action current, and the resistance offered by the tissue traversed, Hill concluded that the energy value of a single action potential wave traversing 1 gm. of muscle, whose fibers are 1 cm. long, is about $23.9 \cdot 10^{-9}$ calorie at 8°C and $6.6 \cdot 10^{-9}$ calorie at 18°C; and the energy value of a single wave passing through 1 gm. of nerve fibers 1 cm. long is about $3.5 \cdot 10^{-10}$ calorie at 6.2°C. In what follows we shall call these the "observed" energies.

From the formula (see chapter I),

$$\lambda_{\mu} = 6.35/T (T + 10) \log Q_{10},$$

one determines the radiation frequency. The energies given at the two temperatures indicate that Q_{10} is 3.55 for the case of muscle, whence the wave length will be $6.35/281.291 \cdot \log 3.55 = 1.41\mu$. The frequency corresponding to this wave length is $2.12 \cdot 10^{13}$, one that lies well within the region of the infra-red, and above the electro-magnetic frequencies, as one may have expected of an electrical action potential. The mean of the observed energies (in the case of muscle $15 \cdot 10^{-9}$ cal.) divided by $h\nu$ will give us the energies in terms of quanta. Thus for

$$\text{muscle } \frac{15 \cdot 10^{-9} \cdot 4.19 \cdot 10^7}{6.55 \cdot 10^{-27} \cdot 2.12 \cdot 10^{13}} = 4.4 \cdot 10^{11}$$

quanta. If we assume further that the law of equivalence holds in these cases then the number of molecules or ions made reactive in the muscle is equal to the quanta engaged, that is, also equal to $4.4 \cdot 10^{11}$. And if the solvent for these ions occupies, say, one-tenth of the gram muscle (in all probability it cannot occupy the whole of the muscle substance) then the concentration of the ions will be about $4.4 \cdot 10^{11}/6.06 \cdot 10^{19}$ or $7.2 \cdot 10^{-9}$ of a gm.-mol. solution.

One may also calculate the effective radiation frequency directly from the observed temperature and Wien's displacement law, and finally the value of one quantum. This into the observed energy of the action current again gives the energy in terms of quanta. The operation is all included in the equation, $q/h\nu = q/b(cT/.2882)$, where again c is the velocity of radiant energy, T the absolute temperature and b Planck's constant; the numeral is the constant in Wien's law. Substituting with the observed data given above one finds that for the action current of muscle at 18°C. , $q = 14 \cdot 10^{11}$; at 8° , $q =$

$5.1 \cdot 10^{12}$ quanta. The energy for the action current of nerve at 6.2°C. , by the same calculation is equal to $7.75 \cdot 10^{12}$ quanta.

If we again assume that Einstein's law of equivalence holds in the case of bio-electric currents then we can further calculate the probable concentration of the ions made reactive, since then, for every quantum a molecule or ion is made reactive and the total number in each case equals the number of quanta. We assumed that only 0.1 of the mass of tissue held the ions affected in solution. The total number in a gm. mol. solution of 1 gm. nerve or muscle then may be put at $6.06 \cdot 10^{19}$. The quanta in each case given above divided by this number show the concentrations to be $2.3 \cdot 10^{-8}$ and $8.4 \cdot 10^{-8}$ gm.-mol. for the muscle at 18 and 8 degrees respectively, and $1/3 \cdot 10^{-7}$ gm.-mol. for the nerve fibers at 6.2 degrees.

Recalling that the concentration of the hydrogen ions in the purest water gives about an $8.5 \cdot 10^{-8}$ gm.-mol. solution, it appears that the concentration of the ions made reactive, as the intenser waves of the electrical action potential sweep over muscle or nerve, is probably no greater than the concentration of those ions in pure water.

2. *The probable number of molecules or ions made reactive in the retinal elements by a minimal effective light stimulus*

Of all forms of stimulation the absolute quantity of light falling on the retina is probably most accurately estimated and hence data from this field of observation are probably best suited for our present purpose.

Of several measurements by different workers as to the minimal light energy necessary to produce a retinal perception one may take those of von Kries and Eyster (18). It will be recalled that in

these experiments the light used was of a mean wave-length, $507\text{ m}\mu$, the part of the spectrum that had already been shown to be most effective for the dark-adapted human retina. The minimal light energy required to produce a retinal perception under optimal spatial and temporal conditions (time exposure of about $1/8$ seconds) was calculated by von Kries to be from 1.3 to $2.6 \cdot 10^{-10}$ ergs. Correcting for probable refractory periods, however, requires a reduction by one-eighth, or to a mean of $2.3 \cdot 10^{-10}$ ergs, as the energy actually made effective.

If we assume that the law of equivalence holds in the photochemical reaction taking place in the retina then we may calculate the number of molecules made reactive in the rods. Light of wave length $507\text{ m}\mu$ has a quantum value of $6.55 \cdot 10^{-27} \cdot 5.9 \cdot 10^{14} = 3.86 \cdot 10^{-12}$ ergs per molecule. The total number of quanta, and therefore molecules, required to absorb the whole of the energy would then be $229 \cdot 10^{-12} / 3.86 \cdot 10^{-12}$, or about 60 molecules.

There is probably a refractory period following every excitation wave set up by the retinal cells. The time of this is not known but it is this factor that determines rhythm rate. By taking one of the higher normal rhythm rates known for excitation waves multiplied by one of the briefer known chronaxie rates we may get a rough measure of the probable time during which the cells are absorbing light. A rhythm rate of 125 times a chronaxie of .001 second indicates a period of 0.125 second out of every second during which the light reaction is being reversed. The effective part of the energy thus becomes only about $7/8$ of the total energy of the incident light, or about $2.3 \cdot 10^{-10}$ ergs, and the probable number of molecules made reactive is again nearly 60.

The interested reader may compare this

result with that of Noddack (22), who calculates that only $30\text{ }h\nu$ or light energy incident upon the eye is required for a minimal visual stimulus; and, assuming that $29/30$ of this is ineffectual, concludes that only $1\text{ }h\nu$ is utilized in the actual retinal stimulus.

It now becomes a matter of further interest to know the approximate concentration of these 60 molecules. Although the data and method of calculation are given in his paper, von Kries does not state the exact areas of the retina illuminated. There is good evidence that the smallest area that can be stimulated, and still give a light perception, must include at least two rods. In the human retina these elements are about 2μ in diameter and 60μ long, and only their outer halves are said to contain the visual purple. The volume contents of these two outer halves being the same as that of one rod, the volume becomes $\pi r^2 h$, or $188\mu^3$. It is hardly likely that the whole of even this small volume is filled with a solvent for the specific light sensitive substance; let us suppose it occupies $1/100$ of the volume, then the volume holding the 60 molecules becomes only $1.88\mu^3$. Since now a gram-molecular solution filling this space requires that $6.06 \cdot 10^{23} \cdot 1.88 / 1.10^9$ or $1.14 \cdot 10^{15}$ molecules are in solution, the concentration represented by the 60 reactive molecules must be $60 / 1.14 \cdot 10^{15}$, or about a $5.5 \cdot 10^{-14}$ gm. mol. solution. The area of the retina stimulated, however, having been an *optimal* area for a minimal stimulating strength, probably was somewhat larger than the one just considered; but the number of molecules according to our postulate remains the same, and, therefore, their concentration even less than the concentration indicated when only two rods are stimulated. For example, if 400 rods instead of two were stimulated

then the concentration would be a $2.7 \cdot 10^{-16}$ gm.-mol. solution. If the case of two rods only be considered then the concentration of hydrogen ions in the purest water appears to be ($8.5 \cdot 10^{-8} / 5.5 \cdot 10^{-14}$), nearly $1.5 \cdot 10^6$ greater than highest probable concentration of the reactive photochemical substance in the retina when stimulated by the least amount of energy capable of evoking a light perception.

The work of Boswell (19) on the minimal light energy falling on the fovea, required to produce a visual perception, gives the desired data somewhat more precisely. The observations were also made in von Kries's laboratory and with nearly the same method and apparatus that Eyster used for the study of peripheral vision. I choose the data obtained with the sodium flame, maximal energy in wave length of $589 \text{ m}\mu$; frequency, $5.1 \cdot 10^{14}$. The minimal area illuminated in four series of observations of different durations appears to have been $.00361 \text{ mm.}$ in diameter, the mean duration of the stimulus $.0061 \text{ second.}$

The cones in the human fovea are known to be about 2μ in diameter by 34μ in length. The illuminated area divided by the area of one cone, or r^2 of the one area by the r^2 of the other, will give the number of cones covered by the incident light. This gives in this case 1.8 cones whose total volume is $1.8 \cdot 1^2 \cdot \pi \cdot 34 = 192\mu^3$. Assuming in the case of the cones the solvent for the photochemical substances occupies only 1/10 of this volume, we have $19.2\mu^3$ in which the molecules or ions are dissolved.

Boswell calculated the energy of the light absorbed by the fovea in the above cases to have a mean value of $31.6 \cdot 10^{-10}$ ergs; allowing for probable refractory periods this should be reduced 1/8, that is $27.6 \cdot 10^{-10}$ ergs. The quantum value of

wave length employed is $6.55 \cdot 10^{-27} \cdot 5.1 \cdot 10^{14} = 33.4 \cdot 10^{-13}$ ergs per molecule, in the case that the law of equivalence holds; whence $27.6 \cdot 10^{-10} / 33.4 \cdot 10^{-13} = 826$ molecules appear to have been made reactive. In this case the concentration of the molecules if dissolved in the volume allowed above will be $826 / 19.2 \cdot 10^{-9} \cdot 6.06 \cdot 10^{23} = 71 \cdot 10^{-15}$ of a gm.-mol. solution, a concentration that is about 1.2 million times more dilute than the hydrogen ions in purest water. The probable concentration of reactive ions in the two cases (of cones and rods) thus turns out to be very nearly the same, however incredibly dilute this concentration appears to be.

3. *Quantum yield in the reduced latent time of a light stimulus as affected by dark adaptation*

In the cases of retinal stimulation just considered I assumed that the law of equivalence was valid, the necessary data to make a quantum yield determination not being available. There are, however, other investigations of sensory mechanisms that give us data for such determination in their respective fields.

It is known that among certain animals the reaction time to a photic stimulus diminishes as dark-adaptation proceeds, and only approaches a constant as this process reaches completion (20). If one subtracts from the gross reaction time that time necessary for the excitation, when once set up, to travel over the reflex arc, then the remaining time must be due to processes going on only in the photo-receptors, a period of time that may be called appropriately the reduced latent time of light stimulation as influenced by dark-adaptation. By observing further the influence of temperature changes on this reduced latent time one obtains a temperature coefficient and may then calculate the reactivity constant, q , the

radiation frequency and finally its quantum value. In his study on influence of temperature upon latent period of dark adaptation Hecht (20) has found that for *Mya arenaria*, $q = 19,700$ cal., between 11.5 and 21.9 degrees C., and for *Pholas dactylus*, $q = 18,300$ cal., between 10.5 and 18.4 degrees C. The quantum yield for *Mya*, $q \cdot 4.19 \cdot 10^7 / Nb(CT) \cdot 2882$, is 6.9 per molecule and for *Pholas* 6.45 per molecule.

4. The quantum yield in the absolute refractory period of nerve stimulation

In all cases of stimuli repeated at intervals sufficiently close there appears the phenomenon known as refractory state. On page 181 of my 1908 paper (7) I pointed out that the observations of Gotch and Burch showed that the refractory period of frog's nerve had a temperature coefficient of about 3.6. Amberson (21) just lately has reinvestigated the phenomenon, confining his attention to the absolute refractory period and using as end-point the least interval required for the appearance of a second electrical response, "which is not further shortened by a considerable increase in the magnitude of the second stimulus." The plotted results "outline a curve which is approximately exponential in form," with a Q_{10} value of 3.06 between 27 and 9 degrees C. Using Amberson's temperature coefficient the energy increment, $q = \log Q_{10} \cdot 457 \cdot 300 \cdot 281 \cdot 4.19 \cdot 10^7 = 7.62 \cdot 10^{11}$ ergs per gm.-mol. The frequency at median temperature is $C \cdot 291 / 2882 = 3.03 \cdot 10^{13}$. Whence, $q / Nb\nu = 7.62 \cdot 10^{11} / Nb \cdot 3 \cdot 10^{13} = 6.25$ quanta per ion, or molecule of the substance made reactive during the absolute refractory period of frog's sciatic nerve.

Thus, for the latent time of dark adaptation and for refractory period of nerve fiber the quanta yield appears to be near

the mean found for the many cases listed in the table at the end of Chapter II. If this quantum yield is also true for minimal retinal stimulation, then the concentrations of molecules or ions taking part in the setting up of that stimulus will be from 3 to 10 times that calculated above, a figure which still leaves the concentration some 2 to 6 million times more dilute than hydrions in purest water.

V

CONCLUSION

The results of the foregoing inquiry are of the kind that clearly indicates the need of further investigations carefully planned and directed towards the determination, as precisely as possible,

(1) As to what constitutes the most elemental response, and recovery therefrom, in living matter when given an adequate stimulus. This may be called the unit of physiological action.

(2) The energy and chemical exchanges, their nature and quantitative relations, at least in the initial and final stages of this unit of physiological action.

(3) The character, quantity and fate of the energy making up the adequate stimulus evoking the unit of physiological action. What part of the energy of such stimulus is lost in the transfer to the effective points in the responsive tissues, what part of it becomes effective?

Indeed may it not be that in the end we shall find that all adequate stimuli at the moment they reach the site of final action are no more nor less than one form or another of radiant energy, and that they evoke responses in living matter in the same manner as light initiates a photochemical reaction in the test-tube, and that the molecules only become "reactive" when the energy they absorb has reached a certain critical value limited by the frequency of the radiation? Indeed the old

Weber-Fechner Law of stimulation could have no more reasonable physical basis. Our perception of increasing stimulating-strength occurs in jumps because the unit of physiological action required at least one quantum of energy to evoke a response.

And yet,—when once this critical difference in frequency has been shown to exist it may well be that the story of quantum relations to non-luminous physiological reactions will turn out much the same way as has the story of photochemical reac-

tions. It may be that only now and then the law of equivalence will be found to hold good, and that as in the purely photo-chemical reactions primary and secondary or even "chain reactions" will have to be invoked to explain the many cases where the law finds no direct application. But if this relation between a clean physiological action and the quantum theorem can be established thoroughly in a single case there will be revealed a control of the forces of life by the most universal of all the known laws of nature.

LIST OF LITERATURE

1. STARK. 1908. *Physik. Zeit.*, 9: 898; EINSTEIN. 1912. *Ann. d. Physik*, 37: 832; WARBURG, E., 1911. *Sitzungsber. d. Kgl. Pr. Akad. d. Wissensch.*, p. 746; 1912, p. 216; BODENSTEIN. 1913. *Zeitschr. f. physik. Chemie*, 85: 329-397. For reviews up to date see KISTIAKOWSKY. 1928. *Photochemical Processes*. Am. Chem. Soc. Monographs, N. Y.; LIND, S. C., 1921. *Chemical Effects of Alpha Particles and Electrons*. N. Y.; NODDACK, W. 1926. In *Handbuch der Physik*, Vol. 23, Chapter 6.
2. VON TAPPEINER. 1907. *Die sensibilisierende Wirkung fluoreszierender Substanzen*. Leipzig; ZWAARDEMAKER. 1912. *Ergeb. d. Physiologie*, xii; 1927, *Hdbch. d. norm. u. path. Physiologie*, 1: 241 and 252 ff; PRATT and EISENBERGER. 1919. *Am. Jour. of Physiol.*, 49: 1; JOLLY, J. 1921. *Phil. Mag.*, 41: 289; 1921, *Proc. Roy. Soc. B92*: 219; CLARK, J. H. 1922. *Jour. Opt. Soc. of Amer.*, 6: 813; WARBURG, O., und NEGELEIN. 1922. *Zeitschr. f. physik. Chem.*, 102: 235; 1923, 106: 191; WEIGERT, 1922. *Ibid.*, 101: 414, 102: 416 and 1923, *Zeitschr. f. Physik*, 14: 383; HARVEY, E. N. 1927. *Jour. of Gen. Physiol.*, 10: 875. For a general review see *Spoehr*. 1926. *Photosynthesis*, Chapter 22, Am. Chem. Soc. Monog. Series, N. Y.; BECKING. 1921. *Radiation and Vital Phenomena*, Utrecht; GURWITCH, A. 1924. *Bull. d'Histol. appliquée*, 1: 486.
3. For review and literature see Rep. and Circular Series of Nat. Res. Council, 1928, No. 81, 1st Rep. of Committee on Photochemistry, also, 1928, in *Jour. Physical Chem.*, pp. 481-575 (April); TOLLMAN, R. C. 1927. *Statistical Mechanics with Applications to Physics and Chemistry*, N. Y., pp. 276-285; LIND, S. C. *Opus cit.* For earlier contributions see TRAUTZ, 1918, *Zeitschr. f. anorgan. Chem.*, 102: 81, and literature cited therein. HABER. 1911. *Ber. d. deutsch. phys. Gesel.*, 13: 1117; PERRIN. 1919. *Ann. Physik*, 11: 1; LEWIS, W. C. M. 1919. *Jour. Chem. Soc.*, 113: 471; LEWIS and MCKAOWN. 1921. *J. Am. Chem. Soc.*, Pt. 1, 43: 1288; LEWIS, G. N., and SMITH. 1925. *Am. Chem. Soc. Journ.*, 47: 1508; RISSE, O. " . . . Röntgenstrahlen," *Ergeb. d. Physiologie*. 1930. 30: 242.
4. BALY. 1913. *Physikal. Zeitschr.*, 14: 893, and LEWIS, W. C. M. 1917. *Chem. Soc. Trans.*, 111: 466, also, 1921, *System of Physical Chemistry*, Vol. III, Chap. VI, London. For a brief review and authoritative comment one may consult BODENSTEIN in *Ergeb. der exakten Wissenschaften*, 1922, Vol. I, p. 207. After summing up the evidence against the thermal radiation theory with the statement, " . . . kurz, der Gedanke, die 'Aktivierungswärme' der Strahlung zu entnehmen, erscheint verfehlt," Bodenstein on the next page makes this hopeful statement: "Hier müssen wir noch alles von der Zukunft erwarten, und es ist zweifellos dass auch hier Plancks Quantentheorie die Führung wird übernehmen müssen . . . Hier darf die chemische Kinetik starke Hilfe erwarten von der Photochemie, und zwar der Photochemie im weitesten Sinne." But see also F. DANIELS. 1928. *Chem. Reviews*, 5: 39-66.
5. MATTHAEI. 1904. *Phil. Trans. Roy. Soc. B.*, 197: 47; HÜFFNER u. GAUSSER. 1907. *Arch. f. (Anat.) u. Physiol.*, p. 209; CAMIS. 1907. *Arch. ital. de Biol.*, 48: 261; TORUP. 1906. *Festskrift Olaf Hammersten*. Upsala Läkare förenings Forhandlingar, N.F. 11. Bd. Suppl.

- BARCROFT and KING. 1909. *Jour. of Physiol.*, 39: 374; BARCROFT and HILL. 1910. *Ibid.*, 39: 411; KUIJPER. 1910. *Rec. trav. botan. Néerlandaise*, 7: 36; MEYERHOF, O. 1912. *Arch. f. gesam. Physiol.*, 146: 157; DU BOIS-REYMOND, R. 1914. *Arch. f. (Anat.) u. Physiologie*, p. 237; WARBURG, O. 1919. *Biochem. Zeitschr.*, 100: 230; OSTERHOUT and HAAS. 1919. *Jour. Gen. Physiol.*, 1: 295; YABUSOE. 1924. *Biochem. Zeitschr.*, 152: 498; GAFFRON. 1927. *Ber. d. deutsch. chem. Gesell.*, Jahrg. 60: 755; HALDANE and SMITH. 1896. *Jour. of Physiol.*, 20: 504; HARTRIDGE. 1912. *Jour. of Physiol.*, 44: 21; HARTRIDGE and HILL. 1914. *Jour. of Physiol.*, 48: li.
6. SNYDER, C. D. 1904. *Biol. Bull.*, 7: 280; 1908. *Amer. Jour. Physiol.*, 22: 330; SNYDER in collab. with FALLUS and ELMENDORF. 1913. *Zeitschr. f. allgem. Physiol.*, 15: 72. See pp. 81 and 82 for data here used. SNYDER, C. D., and ALEIDA VAN'T H. SNYDER. 1920. *Amer. Jour. of Physiol.*, 51: 536; SHAPLEY, H. 1924. *Proc. Nat. Acad. Sci.*, 10: 436; LILLIE, R. S. 1928. *Science*, 67: 596.
7. SNYDER, C. D. 1908. *Am. Jour. Physiol.*, 22: 179; ERLANGER and GASSER in collab. with BISHOP. 1924. *Ibid.*, 70: 640; GASSER. 1928. *Ibid.*, 84: 703; ROSENBERG u. SUGIMOTO. 1925. *Biochem. Zeitschr.*, 156: 266; TANAKI, 1925. *Zeit. f. Biol.*, 83: 399. BROEMSER. 1920. *Biol. Zeitschr.*, 72: 19; LILLIE, R. S. 1920. *Jour. Gen. Physiol.*, 3: 126; CROZIER, W. J. 1925-26. *Ibid.*, 9: 531.
8. SNYDER, C. D., in collaboration with F. W. LIGHT, JR. and N. L. KALTREIDER. 1929. Thirteenth Internat. Cong. of Physiologists, Boston; 1930. *Amer. Journ. of Physiol.*, 92: 117.
9. EVANS, C. L. 1923. *Jour. of Physiol.*, 58: 22. The average of 24 readings given on p. 26 is 0.42 cc. O₂ used per gm. muscle/hour and, I take it, at 37°C. On p. 30 a curve is given of temperature effect on O₂ used, in which the O₂ used at 20°C is put at 0.12 cc.
10. EVANS, C. L. 1926. *Physiological Reviews*, 6: 383, for a table of tensions exerted by a strip of cat's ileum. From my own studies on smooth muscles I find that in the rhythmical contraction 1 gm. smooth muscle exerts a mean of about 30 gm. tension at 20°C.
11. SNYDER, C. D. 1928. *Amer. Jour. of Physiol.*, 84: 69.
12. For this newer "oxidative quotient" see MEYERHOF and SCHULZ. 1927. *Pflüger's Arch.*, 217: 568.
13. VERNON. 1910. *Jour. of Physiol.*, 40: 297; WEIZÄCKER. 1912. *Pflüger's Arch.*, 147: 135; LÜSCHER. 1920. *Zeitschr. f. Biol.*, 72: 108, and 1921, 73: 67; BOHNENKAMP, EISMAYER u. ERNST. 1928. *Zeitschr. f. Biol.*, 87: 489; BARCROFT and DIXON. 1907. *Jour. of Physiol.*, 35: 202; ROHDE. 1912. *Arch. f. exper. Path. u. Pharm.*, 68: 491; STARLING and EVANS. 1914. *Jour. of Physiol.*, 49: 67; FENN. 1928. *Harvey Soc. Lectures*, p. 454. For the data from Barcroft and Dixon the mean rate of beat was assigned arbitrarily to obtain the O₂ used per beat, no rates being recorded in the paper. The hearts being those of puppies and cats the mean rate chosen was put at 160, which may be a little high. If 120 is taken, however, the O₂ used will be increased to 1.6 10⁻⁴ cc., .0193 cc. being the mean of 8 experiments as given on p. 202 of the authors' paper.
14. SNYDER and GEMMILL. 1925. *Am. Jour. of Physiol.*, 73: 564.
15. HILL, A. V. 1928. *Proc. Roy. Soc. B.*, 103: 187.
16. PARNAS, J. 1921. *Biochem. Zeitschr.*, 116: 102.
17. HILL, A. V. 1921. *Proc. Roy. Soc. B.*, 92: 178.
18. VON KRIES. 1907. *Zeitschr. f. Psychologie u. Physiol. der Sinnesorgane*, 41: 373.
19. BOSWELL, F. P. 1908. *Ibid.*, 42: 299.
20. HECHT, S. 1928. *Jour. of Gen. Physiology*, 11: 649.
21. AMBERSON, W. R. 1930. *Jour. of Physiology*, 69: 60.
22. NODDACK, W. 1926. In *Handbuch der Physik*, 23: 625.

CONSTANTS AND SYMBOLS USED IN THIS PAPER

$c = 2.9986 \cdot 10^{10}$ cm/sec, velocity of radiant waves
 $h = 6.556 \cdot 10^{-27}$ ergs/sec, the Planck radiation constant

$N = 6.061 \cdot 10^{23}$, molecules per gm. mol. wt.

$R = 8.315 \cdot 10^7$ ergs/deg. per gm. mol. wt.

or 1.985 cal/deg. per gm. mol. wt.

$C_2 = 1.4300$ (radiation constant of Holborn-Valentiner, E. Warburg, etc.) = Nhc/R

$q = \mu = 2a$, heat of activation in the Arrhenius equation for temperature reaction velocities.

ν = rate of vibration of radiant energy

ρ = Perrin's "universal constant" as used in his "Matière et lumière," p. 20 ff.

$\rho = \frac{1}{2.1} \cdot 10^{-10}$, and is derived as follows: In the

Arrhenius equation, $k = se^{-\frac{a}{T}}$, a is put equal to $\rho\nu$; but since a also = q/R , $q = aR$. The radiation hypothesis of chemical reaction puts $aR =$

$Nb\nu$, from which $a = \frac{Nb}{R} \cdot \nu = \rho\nu$, whence $\rho =$

$\frac{Nb}{R} = \frac{1}{2.095} \cdot 10^{-10}$, a ratio without dimensions.



UNISEXUAL PROGENIES AND SEX DETERMINATION IN SCIARA

By C. W. METZ

*Department of Genetics, Carnegie Institution of Washington, and Department of Zoology,
Johns Hopkins University*

TWO apparently distinct types of reproduction are found in the genus *Sciara*, as indicated by sex ratios. In the one type, which may be designated "digenic," bisexual progenies are produced. In the other, or "monogenic" type, the progenies are essentially unisexual. I am indebted to Prof. E. B. Wilson for suggesting these terms. Different species of the genus appear to differ in respect to mode of reproduction. In some species reproduction is characteristically digenic, in others characteristically monogenic, and in others both types are found. Six species have been studied rather extensively and seven others slightly. The six best known species are divided equally among the three classes on the basis of progenies obtained from wild females.

The fact that two species include strains of both kinds suggests that possibly the other species would reveal both types frequently if sufficient material were secured in nature. This is opposed, however, by the fact that each of the three best known species has been definitely of one type or the other—two monogenic and one digenic. Geographic distribution, so far as observed, is not a factor of importance in this connection. In the case of the three species just mentioned collections have been made in several localities including the northeastern and the southwestern parts of the United States, with uniform

results throughout. In the case of the two species giving both types of sex ratios, on the other hand, the two types were secured from flies taken in the same localities. Within any one species no morphological difference has been detected between individuals or strains of the monogenic type and those of the digenic type, and the two kinds have proved interfertile in crosses.

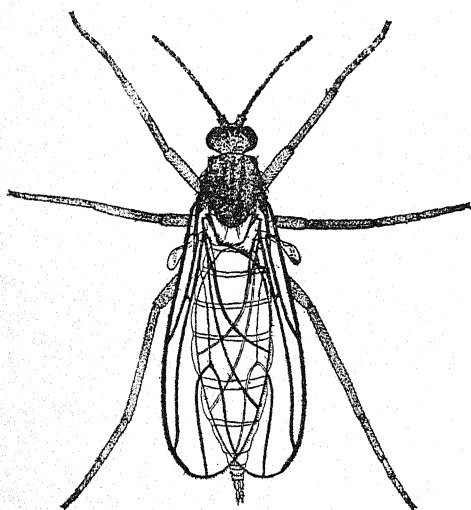
Among the seven species in which relatively few wild specimens have been secured, five are of the monogenic type and two of the digenic. Apparently the monogenic mode of reproduction is the more widespread in the genus, at least as regards American species.

The most noteworthy feature about the sex ratios in the digenic forms is the fact that the proportions of the two sexes vary widely in different progenies instead of conforming to a 1:1 ratio. It is possible that the divergence here is due to differential viability, together with the fact that males emerge before females, on the average; but the evidence weighs strongly against this interpretation. (Details regarding this and other features are to be considered in another paper.) It appears more probable that the ratios here are not modifications of a fundamental 1:1 ratio, but are modifications of the basic 0:1 and 1:0 types found in the monogenic forms. This feature will be considered further below.

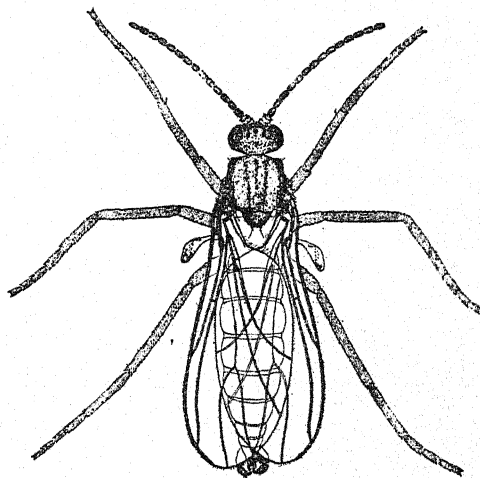
On the other hand, it is not to be concluded that the monogenic and digenic types of reproduction are alike and that the distinction made here is purely artificial. The constancy of the distinction between the two has been shown clearly by study of representative species such as *S. coprophila* Lint., and *S. impatiens* Johan., both of which are typically monogenic, and *S. pauciseta* Felt, which is digenic. In all three of these species progenies have been obtained from many wild females and from

genic strain. This digenic strain descended from a single female and its digenic characteristic has been shown by crosses to be due to a genetic modification distinguishing it from the regular monogenic type. The digenic strain in *S. impatiens* was derived from one wild female and showed the same type of genetic differences from the monogenic strains as did that in *S. coprophila* (unpublished data).

Most of our work has been devoted to a study of the monogenic type of reproduc-



Sciara coprophila ♀



Sciara coprophila ♂

SCIARA COPROPHILA LINTNER. Camera drawings of wild-type female and male; not at same magnification. Actually the female is considerably larger than the male.

many generations of pair matings in the laboratory. Whereas, in the former two species the progenies have been almost exclusively of the "unisexual" type, those in the last species have been consistently of the bisexual type. Furthermore, in both *S. coprophila* and *S. impatiens*, the species studied most extensively, an "exception which proves the rule" has been secured in the form of a digenic strain. That in *S. coprophila* was derived in the laboratory from a pedigreed inbred mono-

tion, using especially *S. coprophila*, and to a lesser extent *S. impatiens*, as material. The following résumé includes the main results of this study up to the present time.

SEX OF PROGENY

In considering sex determination in the broad sense it is necessary at the outset to distinguish between the determination of the sex of the progeny as a whole and that of the individual fly. The sex of the progeny has been shown (Moses and Metz, 1928) to be due to the zygotic constitution

of the female. Female-producing females and male-producing females are ordinarily present in equal numbers in female progenies, showing that the mother is heterozygous for some factor which distinguishes between the two types (Metz and Moses, 1928). Present evidence, although not complete, indicates also that it is the zygotic constitution of the female which makes the distinction between monogenic and digenic modes of reproduction. Genetic studies with the aid of mutant characters have shown that the differential responsible for determining "sex of progeny" is carried by the sex chromosomes (Metz and Schmuck, 1929). Its mode of inheritance is indicated in the accompanying diagram and is discussed below.

SEX OF THE INDIVIDUAL

As noted below, genetic evidence previously reported led to the tentative conclusion that males in *Sciara* are XY in sex chromosome constitution and that the sex of the individual fly is determined by the type of sperm (X- or Y-bearing) which fertilizes the egg. Recent, unexpected cytological evidence, however, has brought to light a chromosome difference between germ-line and soma in the males which suggests an entirely different interpretation of this process. Owing to the fact that neither the genetic nor the cytological line of evidence is complete, as yet, both are reviewed briefly, together with the possible interpretations which they suggest.

(1) Genetic evidence

The genetic studies already mentioned (see also Metz and Ullian, 1929) reveal the presence in these flies of sex-linked inheritance of the type commonly found where the female is XX and the male XY in constitution. It would seem to follow, therefore, that such sex chromosomes are present, although they have not been dis-

tinguished cytologically. The presence of Y is inferred from the fact that in males (spermatogonia) the chromosomes are present in pairs. With females essentially XX and males XY in constitution it would likewise follow that the sex of the individual is "determined" by its sex-chromosome constitution, which presumably is in turn determined by the type of sperm (X-bearing or Y-bearing) fertilizing the egg.

Since individual males will give offspring of both sexes in large numbers, when mated to different females (Moses and Metz, 1928) it is assumed, on this scheme, that males

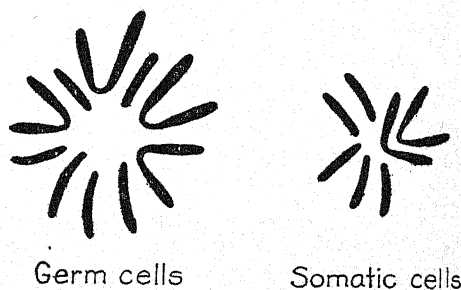


FIG. 1. CHROMOSOME GROUPS IN THE MALE GERM CELLS (SPERMATOGONIA) AND MALE SOMATIC CELLS OF *SCIARA COPROPHILA* LINTNER; DRAWINGS SOMEWHAT SCHEMATIZED

produce and transmit both X-sperms and Y-sperms.

(2) Cytological evidence. Chromosomal differences between soma and germ-line in males

The evidence in this section has been secured entirely from *Sciara coprophila*, Lintner. In former papers it has been stated that in this species the male chromosome group (diploid) includes either ten or nine chromosomes and the female group eight. These counts were made from spermatogonia and spermatocytes in the one case and ovarian cells (probably all follicle cells) in the other. The male group, as described, includes eight chromo-

somes like those in the female, and in addition two (sometimes only one) much larger "male-limited" chromosomes (Fig. 1). Recent examination of somatic tissues in the males of this species indicates that the soma possesses only seven chromosomes—the two "male-limited" chromosomes and one of the rod-like "ordinary" chromosome being absent (Fig. 1). An attempt has been made to complete the comparison by examining the chromosomes in the female germ-line, but without complete success, as yet. Evidence obtained by Mr. Adrian Ter Louw, Miss M. Louise Schmuck and the writer seems to indicate that in many cases the group here is identical with that in the female soma. It seems possible, therefore, that, as formerly supposed, the "male-limited" chromosomes are actually limited to the males, although this is by no means certain. If so, it would appear in the light of the new evidence just considered, that they are limited to the male germ track. Since they almost certainly do not have any direct sex determining function (Metz, 1929, *loc. cit.*) they need not be considered further here.

If the above observations are correct they require the assumption that in males a chromosome elimination takes place from somatic cells (presumably during cleavage) removing the "male-limited" chromosomes and one of the ordinary chromosomes. It seems probable that this process is in some way connected with sex determination and that the "ordinary" chromosome which is eliminated is a sex chromosome. Should this be the case, then two possibilities are presented: If the male is XY in sex chromosome constitution, the Y is evidently regularly eliminated. On the other hand, it is possible, as first suggested to me by my colleague Dr. M. Demerec, that the sex chromosomes of the male are both X-

chromosomes and that the sex of the individual male is "determined" by the elimination of one X from the soma, regardless of the fact that the germ-line (*Keimbahn*) would possess two. Should this be the case, then it is clear from the evidence of sex linkage mentioned above, that it is regularly the paternal X which is eliminated.

Although there is no direct evidence, as yet, in favor of the latter hypothesis, it has the advantage of simplicity. It would avoid the necessity of assuming a process of selective fertilization, which seems to be required by any other scheme (Metz, 1929a) and it would also avoid the necessity of assuming that the sex chromosomes segregate at random while the others appear to segregate selectively at the first spermatocyte division (Metz, 1926, 1929b, p. 492). In addition it would leave the female entirely responsible for the sex determining mechanism, both as regards the individual fly and the "progeny as a whole" where unisexual progenies are obtained (Metz, 1929b).

THE MECHANISM OF SEX DETERMINATION

In the preceding section attention has been devoted especially to the sex chromosomes of the male, showing that, with present evidence, either one of two distinct conditions might exist, depending on whether sex in the male is determined by the process of chromosome elimination just considered, or in the ordinary fashion by the union of a Y-bearing sperm and an X-bearing egg.

Turning to conditions in the female we find much less uncertainty, both as regards the individual fly and the progeny which she produces. From the considerations indicated above (regardless of which of the two alternatives is correct) it appears that the sex of the individual female and

the sex of the progeny as a whole are both "determined" by the same pair of chromosomes—the sex chromosomes. It also appears that the two types of females (male-producing and female-producing) differ in respect to sex chromosome constitution. Genetic evidence has shown (Metz and Schmuck, 1929; Metz, 1929) that in the male-producing female both sex chromosomes are like the X-chromosome of the male, but that in the female-producing female only one is strictly of this kind, the other differing in respect to the differential responsible for "sex of progeny."

This latter chromosome, designated X'

establish it as essentially correct, *as regards the female*. The tests concern the constitution of "exceptional" individuals which appear frequently in "unisexual" progenies. As pointed out in earlier papers (*l.c.*) the "unisexual" progenies in *Sciara* are not exclusively unisexual. A few males occasionally appear in female progenies and a few females in male progenies. Such individuals are designated "exceptions." It is evident from the diagram that "exceptional" males in female progenies should be of two kinds, X (Y?) and X' (Y?). The former should be like ordinary males in constitution and should exhibit

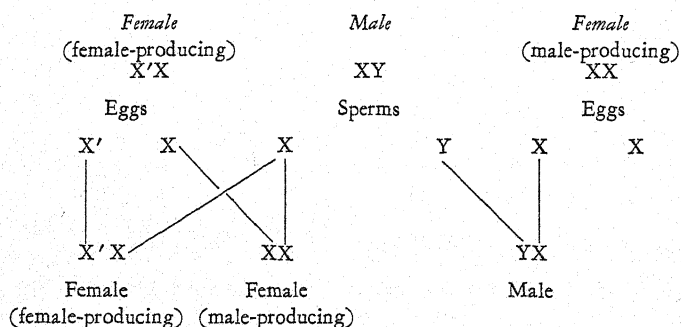


FIG. 2. DIAGRAM ILLUSTRATING SEX CHROMOSOME MECHANISM IN *SCIARA COPROPHILA*

This scheme is especially designed to represent the sex chromosome constitution of the females. As explained in the text the constitution of the male germ-line is as yet uncertain. It may be like that of the male-producing female (XX). In either case the male soma is presumably XO in make up.

to distinguish it from the X, is ordinarily limited, of course, to the one class of females, and does not regularly pass back and forth between females and males as does the X. For the most part, however, it apparently resembles the X in constitution (see below).

On the basis of these observations the scheme shown in the accompanying diagram (Fig. 2) has been proposed as an interpretation of sex chromosome behavior here. So far as the sex chromosomes of the female are concerned this scheme accounts for all the facts thus far observed. Furthermore, it has been subjected to two critical tests which, in our opinion,

the same genetic behavior. The latter, however, should differ and give different results in crosses, due to the presence of X'. When crossed with female-producing females their daughters should all be female-producers, and half of these should in turn give only female-producing daughters. These expectations have been verified by the results (Metz and Schmuck, 1929-b). On the same principle exceptional females in ordinary male progenies should all be of one kind, male producers, because neither parent would contribute an X' chromosome. Here again the expectation has been confirmed (Metz and Moses, 1928).

THE NATURE OF THE X' CHROMOSOME

Since the evidence indicates that the X' chromosome differs from the ordinary X chromosome in these flies, it is of especial interest to ascertain the exact nature of this difference. The data are as yet insufficient for the purpose, but they reveal some features of significance (Metz and Schmuck, 1929). It has been found, e.g., that XX females, X'X females and X'X' females appear to be indistinguishable somatically except by the introduction of mutant characters, and that X(Y?) and X'(Y?) males are similarly indistinguishable. It has also been found that X' carries the normal allelomorphs of the two mutant genes thus far identified in the X. On the other hand we have not succeeded in transferring either of the two genes mentioned to this chromosome—i.e., in combining them with the X' differential. The latter point may have no significance, however, for the two genes exhibit less than 0.5 per cent crossing over in XX females. There is no evidence as yet to indicate whether the differential distinguishing X' from X is a single gene or involves extensive differences between the two chromosomes, but it is clear that whatever the difference between them the two chromosomes are fundamentally similar.

THE CAUSE OF UNISEXUAL PROGENIES

If, as postulated above on the one scheme, the male transmits both X-bearing and Y-bearing sperms and the sex of the individual fly is determined by the type of sperm fertilizing the egg, it is evident that some selective process must operate to cause the progenies to be unisexual instead of typically bisexual.

Differential mortality might account for the observed results; but careful observations (Metz, 1929-b) have indicated that

no such mortality occurs. The only other probable explanation would appear to be that of selective fertilization. On this hypothesis it is assumed that the eggs of female-producing females are fertilized almost exclusively by X-bearing sperms, the Y-bearing sperms being inactivated or eliminated, while in male-producing females the process is just reversed. It is impossible to actually observe such a process in this material, hence the hypothesis cannot be verified by direct observation. The indirect evidence, however, seems to be conclusive providing the assumption of two classes of sperms is correct.

On the other hypothesis, in which sex is determined by the type of chromosome elimination (during cleavage?) unisexual progenies would presumably be produced because the eggs of any one female would all (or practically all) go through the same process of development as regards this feature—either with or without elimination of the one sex chromosome from the soma. Here, as in the preceding case, the end result is determined in advance by the zygotic (sex chromosome) constitution of the mother.

DISCUSSION

Although the analysis of the problems here presented is far from complete, and many puzzling features remain to be cleared up, it may not be amiss at this time to present some tentative considerations on the general aspects of sex determination and sex ratios in *Sciara*. Numerous indications point toward the conclusion that the basic type of reproduction here is monogenic (giving unisexual progenies) and that the digenic type of behavior, found to occur characteristically in some species and more or less frequently in others, represents a modification of this

basic process. Since the monogenic type of behavior apparently depends upon selective fertilization or some other selective action taking place at or after the time of fertilization, it follows that anything interfering with this selection would tend toward the production of bisexual progenies. In the case mentioned above of the digenic strain derived from a monogenic laboratory stock of *S. coprophila*, females of male-producing constitution (XX) are modified so as to give varying numbers of daughters in addition to the expected males (unpublished data). Whether or not the digenic strains and species found in nature are genetically like this strain is not known, but the one found in *S. impatiens* (derived from a single wild female) appears to be of this same type. It would seem probable that various kinds of digenic strains might arise, differing according to the type of genetic changes which had occurred to produce them. On this basis it would be expected that in some cases a change or accumulation of changes would serve to eliminate the selective action entirely and produce strains or species giving typical 1:1 sex ratios. No such forms have yet been detected, but as suggested above this may be due to the presence of differential viability in some of the species studied. The question can be settled only by extensive experiments

with digenic forms under carefully controlled and favorable conditions.

One of the most puzzling aspects of the general problem, if unisexual progenies are due to any such selective action as postulated above, is why this type of reproduction should be so widespread in the genus. It appears to be dependent upon a delicate balance which fortuitous changes (mutations) would be expected to break down, unless some distinct advantage inheres in the process. At present it seems necessary to assume such an advantage to account for the retention of the process in so many species, in spite of the fact that one of the most widespread and apparently successful species (*S. pauciseta*) appears to be consistently digenic in its mode of reproduction.

ADDENDUM

Since this paper went to press further studies on the chromosome group of the female germ-line have indicated that typically this group is like that of the male germ-line, and that the so-called "male-limited" chromosomes are not limited to one sex but to the germ-line of both sexes. (See Metz and Schmuck, Proc. Nat. Acad. Sci. 17: 272, May 1931.)

This investigation has been aided by a grant from the National Research Council, Committee for Research in Problems of Sex.

LITERATURE

- METZ, C. W. Sex determination in *Sciara*. Amer. Nat., 63: 487-496, 1929.
- . Evidence that "unisexual" progenies in *Sciara* are due to selective elimination of gametes (sperms). Amer. Nat., 63: 214-228, 1929.
- . A possible alternative to the hypothesis of selective fertilization in *Sciara*. Amer. Nat., 64: 380-382, 1930.
- METZ, C. W. and MILDRED S. MOSES. Observations on sex-ratio determination in *Sciara* (Diptera). Proc. Nat. Acad. Sci., 14: 930-932, 1928.
- METZ, C. W., MILDRED S. MOSES and ELLEN N. HOPPE. Chromosome behavior in *Sciara* (Diptera) I: Chromosome behavior in the spermatocyte divisions. Zeitsch. f. induk. Abstammungs-u. Vererb., 42: 237-270, 1926.
- METZ, C. W. and M. LOUISE SCHMUCK. Unisexual progenies and the sex chromosome mechanism in *Sciara*. Proc. Nat. Acad. Sci., 15: 863-866, 1929.
- . Further studies on the chromosome mechanism responsible for unisexual progenies in *Sciara*. Tests of "exceptional" males. Proc. Nat. Acad. Sci., 15: 867-870, 1929.
- METZ, C. W. and SILKA S. ULLIAN. Genetic identification of the sex chromosomes in *Sciara*. Proc. Nat. Acad. Sci., 15: 82-85, 1929.
- MOSES, MILDRED S. and C. W. METZ. Evidence that the female is responsible for the sex ratio in *Sciara* (Diptera). Proc. Nat. Acad. Sci., 14: 928-930, 1928.



FORMS OF NITROGEN ASSIMILATED BY PLANTS

By F. E. ALLISON

Bureau of Chemistry and Soils, U. S. Department of Agriculture, Washington, D. C.

IN MUCH of the scientific literature, dealing with plant nutrition, the assumption is made that practically all the nitrogen which plants absorb from soil solutions is in the form of nitrates. It is generally known that ammonia and many organic compounds may be utilized also directly by plants, but the extent to which these are absorbed is usually considered to be very limited except under unusual conditions. It seems that this idea has become prevalent largely for the following reasons: (a) most of the nitrogen in soil solutions is in the nitrate form, and (b) nitrification is supposed to take place so rapidly that soluble nitrogen in forms other than nitrates can not, ordinarily, accumulate. A study of the available information on the subject would seem to indicate to the writer that a considerable portion of the nitrogen assimilated by higher plants, growing in *humid* regions, enters the root in forms other than nitrates. In this article a discussion is given of certain of the more recent investigations of particular interest in this connection.

In a practical consideration of the forms of nitrogen utilized by plants two questions must be considered: (a) what compounds can various plants use under ideal, controlled conditions, and (b) what compounds are available in soils for their use? The first of these questions has been discussed fully elsewhere and will be considered here only to such an extent as to furnish a background for the more interesting discussion of the second question.

FORMS OTHER THAN NITRATES USED UNDER CONTROLLED CONDITIONS

The ability of plants to assimilate many organic forms of nitrogen without nitrification has been repeatedly demonstrated. Hutchinson and Miller (10) have given an excellent review of the work done prior to 1911, as well as much original work, showing that a large number of organic compounds are utilized directly by higher plants. Brigham (3) found that, in general, organic compounds of high complexity are better after ammonification, while the simple compounds are not improved thereby. The work of Schreiner and Skinner (25) showing the utilization of many organic compounds, is also particularly thorough and convincing. The ability to utilize any given compound commonly varies widely with different crops and perhaps even with the same crop under different conditions. Certain investigators have also pointed out that while a given nitrogen source may not produce as good results as nitrate, yet if used in combination with other forms the final results may be better than nitrate alone.

The extent to which plants can utilize ammonia directly is of especial interest since it is the normal end product of the decomposition, of practically all forms of nitrogenous organic matter. The earlier investigations, reviewed by Hutchinson and Miller (11), as well as their own work show that many agricultural plants grow normally when limited to ammonia

nitrogen, but that some plants seem to prefer nitrates. Pantanelli and Severini (16, 17) state that ammonia is more suitable for the formation of organic compounds than is nitrate. Best results were secured with those ammonium salts having anions that possess a nutritive value. Prianchnikov (19, 20, 21) and co-workers have also been leaders in this field of research and have stressed the necessity of adequate control of pH of culture solutions containing ammonium salts.

Jones and Shive (14, 15) secured better growths of wheat and soy-beans in nutrient solutions containing both ammonia and nitrates than in nitrate alone, provided the iron supply was adequately controlled. Prince, Jones and Shive (22) found that soy-bean plants, when given both ammonia and nitrates, preferred ammonia during the early period of growth and nitrate at a later date. Other work done at the same laboratory by Jones and Skinner (13) gave similar results. They showed further that ammonia nitrogen is readily absorbed from solution by the soy-bean plant even when the nitrate nitrogen content of the medium is several times as great as the ammonia nitrogen content. The absorption of ammonia nitrogen did not materially increase with increase in concentration of the ammonium salt in solution; on the other hand, where the nitrate concentration of the solution was increased the absorption of the nitrate by the plants did increase markedly.

Recently Pirschle (18) reported that plants usually gave as good growths on ammonia as on nitrates if the reaction was kept constant at pH 6, while nitrates produced higher yields at pH 4.5 and 7.5.

An experiment by the writer, not previously reported, dealing with ammonia utilization by corn may be of interest here. The system recommended by Wil-

son (28) for growing plants under sterile conditions, was adopted with slight modifications. The seeds were sterilized by adding warm alcohol or acetone, mercuric chloride, and finally sterile water. The plants were grown in one liter bottles, containing a culture medium of the following composition, expressed as grams per liter: CaCl_2 — 0.45; KH_2PO_4 — 0.167; MgSO_4 — 0.167; KCl — 0.083; FeCl_3 — 0.001; and CaCO_3 — 1.0. To this medium was added 100 mgm. nitrogen per liter in the various forms. The dry weights of both the tops and roots of the corn plants are given in Table 1, the harvesting being done 90 days after germination when the tassels were just beginning to appear. In the case of calcium nitrate only one result is given due to breakage of the duplicate bottle.

In considering the results given in Table 1, it should be emphasized that in order to reduce the chances of contamination the culture solutions were not changed or aerated during the growth period. The experiments were planned as a qualitative study of the response of the plants to nitrates and ammonia. It was realized that a strictly quantitative comparison would require the use of a larger number of plants, provision for periodic changing of the culture solutions, and the addition of the nitrogen at intervals.

The dry weights of the corn plants show that there is no reason to suppose that nitrate nitrogen is necessary for the normal growth of the corn plant, or that it is superior to ammonia nitrogen. This was true regardless of the fact that the ammonium sulfate was used at a concentration sufficiently high to cause a decidedly retarded growth for the first three weeks. At the end of the experiment there was no appreciable difference in appearance of the plants grown with

ammonium sulfate alone and those with the ammonium sulfate-sodium nitrate combination. The growth with sodium nitrate alone was rather disappointing due, probably, to the excess of sodium, which would affect the absorption of other ions. Calcium nitrate produced growth markedly superior to sodium nitrate but not equal to ammonium sulfate. Ammonium phosphate was not nearly as satisfactory a source of nitrogen as ammonium sulfate, but was slightly superior to sodium nitrate. The various forms of nitrogen used showed little differ-

it is not thought that the organisms appreciably affected the results.

Analyses for total nitrogen showed that the plants assimilated practically all of the nitrogen available regardless of the form in which it was supplied. The nitrogen content of the dry matter produced, therefore, varied inversely with the quantity produced.

FORMS USED UNDER FIELD CONDITIONS

On the previous pages evidence is presented to show that most higher plants can assimilate ammonia and a large vari-

TABLE I
Dry weights of corn plants

TREATMENT	TOPS	AVERAGE	ROOTS	AVERAGE	TOTAL	AVERAGE
	<i>gms.</i>		<i>gms.</i>		<i>gms.</i>	
No nitrogen	1.02 .87	.95	.72 .65	.69	1.74 1.52	1.63
Ammonium sulfate	8.75 10.40	9.58	1.68 3.60	2.64	10.43 14.00	12.22
Sodium nitrate	6.25 6.36*	6.31	1.80 2.05	1.93	8.05 8.41	8.23
Ammonium sulfate 50% Sodium nitrate 50%	9.16 10.22*	9.69	2.99 2.86	2.93	12.15 13.08	12.62
Calcium nitrate	8.30	8.30	3.46	3.46	11.76	11.76
Ammonium phosphate	7.19 6.45*	6.82	2.13 1.35	1.74	9.32 7.80	8.56

* Contaminated.

ences in their effects on the time required to reach a certain stage of growth.

Tests for sterility, made on all solutions at the end of the experiment, showed that three of the bottles, designated in Table I, contained a limited number of fungi. These contaminations were barely visible to the eye and apparently did not occur until about two weeks prior to the end of the experiment. Since fungi do not form nitrates, and since the infected cultures produced approximately the same growth of corn plants as the duplicates,

ety of organic forms of nitrogen in addition to nitrates. The main question is whether plants have available for their use any appreciable quantity of soluble nitrogen other than nitrates. Strictly quantitative information on the subject is necessarily meager because of the difficulties involved in such experimentation. There is a mass⁹ of information available, however, of an indirect nature that serves as a basis for judging what is taking place under field conditions. A few of the outstanding facts, particularly with regard to ammonia, are presented below.

Nitrates and Nitrites

Under average soil conditions most writers consider that nitrates are the chief, and in most cases almost the only, source of nitrogen for plants other than the legumes and a few unusual crops. Many studies have also been reported which apparently show that there is a correlation between crop growth and the nitrifying power of a soil. Such studies, as Gainey (8) has pointed out, often imply that fertility is more or less limited by the processes of nitrification. A careful analysis of the subject, however, led Gainey to conclude logically that "while nitrification is perhaps a valuable and even essential asset in fertility it probably does not, under normal conditions, become a limiting factor in productivity." He considers that fertility in normal agricultural soils in so far as nitrate nitrogen is concerned is limited by those processes necessarily preceding nitrification rather than by nitrification itself. Burd (5) also speaks of the tendency of students in soil biology "to regard determinations of the concentration or rate of formation of some specific end product of soil activities, such as nitrate, as conclusive of the effect upon soil fertility of the processes involved; whereas the author (Burd) has long believed that these latter have a more general significance." It is rather surprising that this view is not more generally held.

A thorough discussion of nitrate assimilation by plants seems unnecessary. No doubt nitrate nitrogen is the best source of nitrogen for the majority of plants and under conditions where nitrates are present in relatively high percentages, or where the conditions for rapid nitrification are favorable, it is safe to say that most of the nitrogen assimilated is in this form. Such ideal conditions, however,

do not exist in the majority of soils, or even in the very best of soils throughout the year.

Nitrites may also be utilized by higher plants where the concentrations are low but they are so rapidly oxidized to nitrates that they ordinarily occur only in traces in soils and there is little reason for believing that plants secure much of their nitrogen in this form.

Organic nitrogen

Amino-acids and other simple water-soluble forms of organic nitrogen are intermediate products in the breaking up of proteins into ammonia. We know that ordinarily there is no accumulation of such compounds in soils because the microorganisms present use them for food. They either convert them into protein or break them up and discard ammonia as the end product. Higher plants do, no doubt, actively compete for the small quantities of soluble organic nitrogen but we know little about the quantities that they assimilate.

Ammonia

Ammonia, which is constantly being formed in soils, may or may not accumulate in appreciable quantities, depending upon conditions. In the discussion which follows, the subject will for convenience be considered under two headings—(a) special conditions, and (b) normal conditions.

Special conditions:—A few plants are known to thrive and produce normal growths where nitrification is practically impossible. Rice, for example, thrives on flooded lowland soils and responds better to applications of ammonium salts than to nitrates. Janssen and Metzger (12) state that it seems fairly well established that nitrate nitrogen does not perform a major rôle in the nutrition of rice

plants because (a) nitrates are reduced in a submerged soil and are nearly completely removed, and (b) the rice plant clearly prefers ammonia to nitrates as a nitrogen source. Many other plants are known to grow under similar conditions.

Hutchinson and Miller (11) make the following interesting comment regarding certain of the Rothamsted plots which 100 years ago contained an abundance of CaCO_3 .

It has recently been shown that the soil of some of the Rothamsted grass plots which have received ammonium salts for many years in succession has become distinctly acid and that, consequently, nitrifying organisms have become greatly reduced in numbers. Nitrification is limited to portions of soil directly in contact with the few particles of CaCO_3 still remaining in the soil. It is evident, therefore, that more or less of the nitrogen assimilated by the grasses must be in a form, or in forms, other than nitrate—probably mainly an ammonium salt.

Other information in substantiation of this idea has been supplied by Russell and Hutchinson (24). They showed that soils partially sterilized by heat or toluene produced larger crops of rye than did the untreated soils. They showed further that the treatment killed the nitrifying organisms but ammonia production was markedly stimulated. They attributed the increased productiveness of a partially sterilized soil to this increase in amount of ammonia present, which in turn resulted from bacterial action.

White (27) refers to the work of certain early investigators who found that forest soils do not contain nitrates, presumably because the acidity is too high for nitrification.

Albrecht (1, 2) made a study of soils under straw mulches and found that usually little nitrate accumulated because of excessive moisture and poor aeration. The ammonia content was higher in such soils, however, being as great as 22 p.p.m. in some cases. This is significant con-

sidering that many crops, particularly corn and potatoes, are known to grow unusually well under such conditions.

Stewart, Thomas, and Horner (26) made studies with pineapple plants from which they concluded that this crop is capable of assimilating all of its nitrogen in the form of ammonium salts. The authors were of the opinion that their data suggested that under field conditions the pineapple plant uses nitrogen in both the nitrate and ammoniacal forms.

It is common practice also to grow many crops on rather acid soils either because the crops prefer such soils or perhaps for the sake of controlling diseases. Potatoes, for example, are often fertilized with ammonium salts and the soil kept acid to control scab. Many other such special cases might be given where we are fairly certain that much of the nitrogen enters the plant in forms other than nitrates. It is not meant to imply, however, that no nitrification takes place in acid soils. Nitrates may be formed, as White (27), Fred and Graul (7), and many others have shown, but the process is greatly retarded.

Normal conditions:—Most soils contain comparatively small amounts of ammonia. Gainey (8) has summarized a considerable portion of the data reported prior to 1917. These results show variations from 0 to 69 p.p.m. with the majority of the figures between 5 and 20. In a few cases the percentage was higher than that of nitrates. Ammonia determinations made by Russell (23) on certain Rothamsted soils show that during the cold spring months ammonia may persist for several days or weeks following applications of ammonium salts or stable manure, but rapidly decreases when the soils become warm. Ordinary soils were found to contain about one or two parts per million, while rich soils contained 3 or 4. Using Russell's figures, an acre-foot of soil com-

monly contains 3 to 12 pounds of ammonia nitrogen; using American data these figures are considerably higher. The methods of ammonia analysis, used in the past, were not very accurate and allowance must be made for this fact in considering the data.

While quantitative data showing the ammonia content of soils are of interest the figures are likely to be misleading unless it is borne in mind that ammonia rarely accumulates to any extent; *it is constantly being formed and constantly being removed*. The total ammonia produced in an acre-foot of soil during a year might easily be as high as 200 pounds and yet an analysis might not show more than 2 to 5 p.p.m. at any given time. We know, however, that the soil tends to establish an equilibrium so as to maintain the ammonia content at a fairly constant minimum. A variety of agencies or factors are responsible for the disappearance of the ammonia, the chief of which are: (a) oxidation by nitrifying organisms, (b) utilization for growth by microorganisms, (c) assimilation by higher plants. A very slight loss may result from leaching and volatilization. Too often nitrification is about the only factor stressed.

It has frequently been claimed that nitrification is more rapid than ammonification, otherwise ammonia would accumulate in soils. This is probably true for most soils but only because the ammonifying organisms are limited to rather inert organic materials as food. If a considerable quantity of a material, such as dried blood, is added then ammonification may become 10 to 1000 times as rapid as nitrification. Very high percentages of ammonia (1500 p.p.m. or more) may accumulate with only traces of nitrates formed during short incubation periods (3 to 7 days). On the other hand, if we add ammonium salts to soils in

optimum concentrations nitrate formation is relatively slow. Ammonification is, therefore, inherently a far more rapid process than nitrification. The chief reason for the differences in rates is that two types of compounds and two groups of organisms are involved. The foods used by the ammonifiers may be considered as essentially combinations of carbohydrates and ammonia. They attack these compounds (proteins, amino-acids, etc.) primarily in order to get the energy of the carbohydrate and incidentally liberate the ammonia. On the other hand, the nitrifiers attack the ammonia in order to obtain energy by oxidation of the ammonia, itself, rather than associated materials. In both cases energy is the chief thing desired by the organisms and it merely happens to be the case that under ideal conditions one energy-producing process is much more rapid than the other.

The disappearance of ammonia from soils as a result of the growth of soil microorganisms, other than the nitrifiers, is due to the fact that these organisms require available nitrogen for the construction of their own body protein. Most of these grow just as well, or even better, with ammonia as with nitrates. The quantity used by these organisms varies widely with the numbers present, temperature, food supply, etc. If organic matter that has a very high carbon-nitrogen ratio is being rapidly decomposed, very frequently almost all traces of all forms of soluble nitrogen are used; if the ratio is low, then the decomposition processes commonly result in the liberation of more ammonia than is needed by the organisms themselves.

Our knowledge of the quantity of ammonia assimilated by higher plants growing in field soils is very limited. Analyses of soils for ammonia might indicate that it is of little importance, but the

fact that it rarely accumulates does not justify such a conclusion. Even the nitrogen assimilated by higher plants as nitrate must first pass through the ammonia stage, where both higher and lower plants compete for it. We know that both groups of organisms can remove practically the last traces from the soil solution. We know, furthermore, from the work of Prianichnikov (21), Shive and his co-workers and many others that ammonia is absorbed by plants at a very rapid rate—more rapidly than nitrifying bacteria can oxidize it. To these facts we should add the very important findings of Jones and Skinner (13), previously mentioned, that certain plants decidedly prefer ammonia during the early stages of their growth. Burd (4) has shown that in the case of a crop such as barley most of the nitrogen required by the plant for its entire growth is assimilated during the period of 6 or 7 weeks beginning when the plant is 3 weeks old. Assuming a normal nitrogen supply the quantity absorbed is roughly proportional to the green weight of the plant during this growth period; with an excess of nitrogen the young plant will store it up to a considerable extent.

Nitrification ordinarily proceeds rather slowly in humid regions during the spring months when crops require the most nitrogen. This is particularly true in the North, where the temperature effect is intensified by the fact that most of the soils are rather heavy; hence they retain more water and for longer periods following rains than do the soils of the South, which are largely sandy. Even the total supply of all forms of available soil nitrogen is usually not sufficient for the optimum growth of plants in the early spring. Burd (4), Burd and Martin (6) and Hoagland (9) have stressed this point. This

fact is so well known and so general that the use of nitrogenous fertilizers for speeding up the growth of early crops, especially leafy vegetable crops, is almost universal. Even in the South the same practice is recommended for cotton in order to hasten plant development and lessen boll weevil injury. Too low a temperature, high acidity, poor aeration, or excess of organic matter may greatly retard nitrification. In addition, where the rainfall is heavy, denitrification may be a considerable factor. Under such unfavorable conditions ammonification may be retarded also but to a less extent than nitrification. If both processes are slow, higher plants can still use ammonia supplied as a fertilizer. Many soils which might nitrify sufficiently rapidly to produce enough nitrate to supply the plant needs if given the entire season, certainly can not fully meet those needs if given only a period of about two months during the spring season to do it. Is it likely that plants growing in soils deficient in nitrates fail to assimilate ammonia (constantly being formed or added in fertilizer) and other protein decomposition products, particularly when practically all of these are excellent plant foods?

In closing, it is well to state that while emphasis has been placed on the direct absorption of forms of nitrogen other than nitrates, it is not to be assumed that nitrates are of minor importance. So much emphasis has always been placed on nitrates that there is no need for further facts along this line. The writer has merely taken for granted that under average field conditions nitrate nitrogen is probably the most important nitrogen source for crops, but has pointed out that other forms may also be utilized to a greater extent than has generally been supposed.

SUMMARY

1. A brief review is given of previous investigations dealing with the forms in which nitrogen can be utilized by plants. In addition to nitrates it is shown that many organic forms of nitrogen and ammonia are assimilated by higher plants. Many recent investigators have found that ammonia is usually as satisfactory a direct source of nitrogen for plants as nitrate, provided the H ion concentration is kept low; while some plants, especially when young, decidedly prefer ammonia.

2. A report of an experiment with corn, grown in solution cultures with various ammonium salts in comparison with nitrates, showed that under the conditions

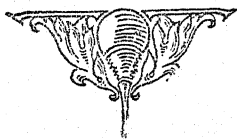
there was nothing to indicate that nitrate nitrogen was necessary for the normal growth of corn or was superior to ammonia nitrogen.

3. A discussion of ammonia utilization by plants grown in field soils is given. It is pointed out that there is very little information on this point, but the available facts seem to indicate that a greater percentage of the nitrogen assimilated by higher plants under field conditions may be taken up in forms other than nitrates than is generally supposed. This is particularly true in the humid regions where the majority of the soils are acid, where the rainfall is heavy in the spring, and where the soil warms up rather slowly.

LIST OF LITERATURE

1. ALBRECHT, W. A. Nitrate accumulations under the straw mulch. *Soil Sci.*, 14 (1922), 299-305.
2. ALBRECHT, W. A., and UHLAND, R. E. Nitrate accumulations under straw mulch. *Soil Sci.*, 20 (1925), 253-268.
3. BRIGHAM, R. O. Assimilation of organic nitrogen by *Zea mays* and the influence of *Bacillus subtilis* on such assimilation. *Soil Sci.*, 3 (1917), 155-195.
4. BURD, J. S. Rate of absorption of soil constituents at successive stages of plant growth. *Journal Agr. Research*, 18 (1919), 51-72.
5. ———. Relation of biological processes to cation concentrations in soils. *Soil Sci.*, 20 (1925), 269-283.
6. BURD, J. S., and MARTIN, J. C. Some mutual effects on soil and plant induced by added solutes. *Calif. Agr. Exper. Sta. Tech. Paper No. 13* (1923), 27 pp.
7. FRED, E. B., and GRAUL, E. J. Some factors that influence nitrate formation in acid soils. *Soil Sci.*, 1 (1916), 317-338.
8. GAINES, P. L. The significance of nitrification as a factor in soil fertility. *Soil Sci.*, 3 (1917), 399-416.
9. HOAGLAND, D. R. Physiological aspects of soil solution investigations. *Hilgardia*, 1 (1925), 227-257.
10. HUTCHINSON, H. B., and MILLER, N. H. J. The direct assimilation of inorganic and organic forms of nitrogen by higher plants. *Cent. Bakt. (etc.)*, 2. Abt., 30 (1911), 513-547; *Journ. Agr. Sci.*, 4 (1912), 282-302.
11. HUTCHINSON, H. B., and MILLER, N. H. J. Direct assimilation of ammonium salts by plants. *Journ. Agr. Sci.*, 3 (1909), 179-194.
12. JANSSEN, G., and METZGER, W. H. Transformation of nitrogen in rice soil. *Journ. Amer. Soc. Agron.*, 20 (1928), 459-476.
13. JONES, C. D., and SKINNER, C. E. Absorption of nitrogen from culture solutions by plants. *Rpt. of Dept. of Plant Physiol.*, N. J. Agr. Exper. Sta. 1926, 360-365.
14. JONES, L. H., and SHIVE, J. W. Effect of ammonium sulfate upon plants in nutrient solutions supplied with ferric phosphate and ferrous sulfate as sources of iron. *Jour. Agr. Res.*, 11 (1921), 701-728.
15. ———. Influence of ammonium sulfate on plant growth in nutrient solutions and its effect on hydrogen-ion concentration and iron availability. *Ann. Bot.*, 37 (1923), 355-377.
16. PANTANELLI, E., and SEVERINI, G. Some experiments on the utilization of ammonium salts by green plants. *Staz. Sper. Agr. Ital.*, 43 (1910), 449-544. *Abs. in Expt. Sta. Rec.*, 25, 223.
17. ———. Further experiments on the utilization of ammonium salts by green plants. *Staz. Sper. Agr. Ital.*, 44 (1911), 873-908. *Abs. in Expt. Sta. Rec.*, 27, 634.
18. PIRSCHLE, KARL. Nitrate und Ammonsalze als Stickstoffquellen für höhere Pflanzen bei konstanter Wasserstoffionenkonzentration. *Planeta*, 9 (1929), 84-104.
19. PRIANICHNIKOV, D. N., and SHULOV, I. S. The

- synthetic formation of asparagin by plants. Zhur. Opytn. Agron. (Russ. Journ. Expt. Landw.), 11 (1910), 533-543. Abs. in Exper. Sta. Rec., 24, 629.
20. PRIANICHNIKOV, D. N. Sur l'assimilation de l'ammoniaque par les plantes supérieures. Compt. rend. Acad. Sci. (Paris), 177 (1923), 603-606.
21. ——. Sur l'assimilation de l'ammoniaque par les plantes supérieures. Revue Générale Botanique, 36 (1924), 5-11.
22. PRINCE, A. L., JONES, L. H., and SHIVE, J. W. Notes on differential ion absorption by plants in relation to reaction changes in nutrient solutions. Rept. of Dept. of Plant Physiol., N. J. Agr. Expt. Sta. 1922, 378-383.
23. RUSSELL, E. J. The ammonia in soils. Journ. Agr. Sci., 3 (1910), 233-245.
24. RUSSELL, E. J., and HUTCHINSON, H. B. The effect of partial sterilization of soil on the production of plant food. Journ. Agr. Sci., 3 (1909), 111-144.
25. SCHREINER, O., and SKINNER, J. J. Nitrogenous soil constituents and their bearing on soil fertility. U. S. Dept. Agr. Bur. Soils Bull. 87 (1917), 1-84.
26. STEWART, G. R., THOMAS, E. C., and HORNER, J. The comparative growth of pineapple plants with ammonia and nitrate nitrogen. Soil Sci., 20 (1925), 227-242.
27. WHITE, J. W. Annual reports 1913-1917, Penn. State Agr. Expt. Sta.
28. WILSON, J. K. Device for growing large plants in sterile media. Phytopathology, 10 (1920), 425-29.





THE VACUUM TUBE OSCILLATOR IN BIOLOGY

By G. MURRAY MCKINLEY AND JOHN G. MCKINLEY, JR.

Zoological Laboratories, University of Pittsburgh

WE ARE already familiar with the far reaching effects obtained in biology by the use of gamma rays, of x-radiation, of ultra-violet, of light and of infra-red. We know that all of these form one great, continuous spectrum of electromagnetic waves, the various regions of which differ only in wave-length. Beyond the near infra-red, as we know, is the radiation used by radio, which extends this spectrum into regions of very long waves, now commonly called Hertzian or electric waves.

Although this spectral band is continuous there are still gaps not yet adequately filled by instrumental means, as, for example, the gap between x-rays and ultra-violet. Another great gap, now being rapidly filled, lies between the near infra-red and the waves of wireless. It is only recently that short wave radio transmission became possible and this advance has led to a continued reduction in the length of waves obtainable. This has largely been made possible by improvement of the three electrode vacuum tube.

The invention of this tube has been the door which opened to the biologist a whole new world of radiation. The region is inconceivably vast, extending, as we know, from the near infra-red to a theoretical infinity, and it might seem quite difficult for him to decide upon some locality as most suitable and promising for experimentation were it not for certain practical and mechanical restrictions. The

limitations of the vacuum tube make it very difficult to obtain wave-lengths of much less than a meter, so that the region of shortest electric waves cannot at present be explored. Again, apparatus generating wave-lengths much longer than 100 meters is not convenient in biology; and the experimenter has for the time being confined his research to a range of wave-lengths of from 1 to about 100 meters.

It is here, then, in the region of relatively short electric waves that we find the biologist utilizing the modern development of the vacuum tube and associated oscillating circuits. He is using equipment ready at hand, easily obtained and at much lower cost than almost any other physical apparatus. Properties inherent in the vacuum tube permit him to select a definite wave-length and to maintain that wave-length in relatively pure form throughout the duration of his experiment. In this way he may probe with some confidence the properties of various wave-lengths within the range of his apparatus. This is not the case in the usual type of high frequency apparatus used for therapeutic purposes—diathermy. Here, the oscillations are produced by condenser discharge through a spark gap. The oscillations produced in this way are a composite of many waves of various lengths, and consistent operation at the wave-lengths worked with in the experiments here reported is impossible.

The biological effects of high frequency oscillations generated by the vacuum tube

appear to have been first investigated by Gosset and his co-workers only six years ago, but since that time much of great promise has been accomplished by biologists in widely separate fields of research—the production of artificial fevers; the attenuation of diphtheria toxin; the treatment of malignant tumors; the acceleration of plant growth; the study of nervous reactions, of respiration and of tissue regeneration.

Gosset, Gutmann, Lakhovsky and Magrou, 1924, studied the effects of very high frequency radiation upon plant tumors caused in the geranium by *Bacterium tumefaciens*. They reported that three geranium plants bearing tumors caused by inoculation with the bacterium were exposed to radiations emitted at a frequency of 150,000,000 cycles per second. The plants were given various exposures on consecutive days and after 16 days from the first exposure the tumors, after growing in the interval, began suddenly to necrose. The necrotic process was said to be complete in about 31 days, so that the tumor could be detached by slight traction. In 16 control plants the tumors grew rapidly to enormous size and recurred after surgical excision.

Schereschewsky, 1926, seems to have been the first to subject animals to the action of high frequency oscillations generated by the vacuum tube. He placed small laboratory animals (mice) in a box of insulating material held in the field of a condenser resonating a tuned circuit. He found that exposure caused severe symptoms which might result in death if the exposure was prolonged more than a few minutes. Part, at least, of these symptoms he thought to be due to heat retention. Besides this acute lethal effect, exposure, he found, caused destruction of tissue. After sublethal exposures, in many instances, small hemorrhagic areas were

observed along the course of blood vessels of the ears and within a few days the ears became necrotic and dropped off. This was also true of the tail. He believed that his experiments indicated a differential action with respect to frequency and that frequencies of highest lethality lay between 18,000,000 and 66,000,000 cycles per second. Finally, he remarked that here was a band in the spectrum of radiant energy which as yet had been little studied in its effects on living cells.

In his first paper, 1926, Schereschewsky described in detail the construction of his apparatus. For the more important of his experiments he used the type of oscillator originated by Huxford, 1925. Christie and Loomis, 1929, continued these descriptions of suitable circuits for biological experimentation and McKinley, 1930, described a convenient apparatus for treatment of small laboratory animals and materials. Unlike most physical apparatus the high frequency generator is surprisingly easy to assemble, and this in itself gives promise of its wide application in biology.

In all of these circuits the experimental animal, insulated in a box of nonconducting material, is placed in the field between the plates of a condenser which is part of a circuit excited by the oscillator at some particular frequency. Consequently, as pointed out by Schereschewsky, no free electrons from the external metallic parts of the circuit can enter, nor can they flow out from the body of the experimental animal. The animal, however, is subjected to a displacement current, in which electrons in the molecules of the body cells will, according to their state of freedom, either pass from molecule to molecule, first in one and then the other direction, or, if bound, are stressed in a direction the polarity of which alternates at the oscillator frequency.

THE TREATMENT OF MALIGNANT TUMORS

Schereschewsky believed that frequency was an important factor in the action of these oscillations and the thought occurred that, under suitable conditions, oscillations at certain frequencies might prove more injurious to some tissue cells than to others. To test this he chose the tissue cells of transplantable tumors because here he had groups of cells distinctly different from adjacent body cells, not only in size but in rate of proliferation. He selected for his experiments a most virulent mouse sarcoma, implantation with which yielded 95 to 96 per cent of takes. Treatment was localized as far as was possible to the cancer cells, the tumor being placed between small insulated plates. Frequencies from 60,000,000 to 150,000,000 cycles per second were used.

Soon after beginning his experiments he noted that in favorable cases treatment had a pronounced effect upon the tumor, the mass seeming to become much smaller and softer almost immediately after exposure. In these favorable cases the tumor and affected area around it came away within 10 days to 2 weeks, leaving the skin pink and healthy beneath it. Many technical difficulties arose during the course of these experiments but the most troublesome was the association of this tumor with a diphtheroid bacillus, which of itself is pathogenic for mice. Many mice were lost from this cause even after the tumor had apparently receded completely. However, despite all difficulties, of 403 mice which he treated 100 recovered tumor free. No case of spontaneous recession of the tumor was observed in 230 control mice, all of which died in from four to six weeks from the date of implantation. Schereschewsky and Andervont, 1928, performed similar experiments upon a transplantable fowl sarcoma. The tumors were im-

planted in the skin and combs of adult chickens, several of the birds being used many times after having recovered from successive implantations. In these experiments 61 per cent of the tumors receded completely.

So much for the brighter side of this picture. Christie and Loomis, 1929, in a very careful study of the effects of high frequencies on mouse sarcoma were unable to duplicate the promising results of Schereschewsky. Their experiments led them to believe that treatment in the high frequency field was not only ineffective in controlling tumor growth but that there was no evidence to support the contention that there is a differential action upon tissue cells with respect to frequency. They were impressed with the fact that the lethal effects of exposure in the high frequency field seemed to be due entirely to retention of heat to a degree incompatible with life. Kahler, Chalkley and Voegtlin, 1929, were also impressed with this heating effect and came to the conclusion that the only demonstrable effect, as far as their material was concerned, was primarily caused by a temperature increase in the organism. They worked with a protozoan (*Paramoecium caudatum*).

IS THERE A SPECIFIC ACTION APART FROM HEAT PRODUCTION?

The ultimate value of the high frequency field in cancer research is, then, an open question, as is its possible differential action on various tissues of the body. At the moment investigators in the field seem to be more concerned with the observed heating effects, a matter of undoubted importance, for, if the effect is purely one of heat, it might seem rather useless to obtain it in this way. The generation of heat is probably due, as has been pointed out, to severe displacement currents set up in the body of the animal by the action

of the field. The heat is, of course, internal and has been used, as will be seen later, to obtain any degree of synthetic fever. Consideration of the high frequency field from a purely physical point of view might lead one to expect, *a priori*, that it would be possible, providing one used the proper material, to demonstrate a secondary effect independent of the heat factor. This, it seems, is just what at least one experimenter has shown.

Szymanowski and Hicks, 1930, working at 158,000,000 cycles per second have been able to definitely attenuate diphtheria toxin without elevating the temperature to a level which would by itself affect the toxin. The control in this experiment was very carefully worked out and the results so uniform as to leave little doubt that there is a specific action of short electric waves other than the heat produced by conductivity and eddy currents. These two experimenters are now interested in the action of the high frequency field on the two other major toxins, botulinus and tetanus, and in the suggestion of D'Arsonval that the irradiated diphtheria toxin should be investigated with regard to its properties as an immunizing substance. McKinley, 1930, also obtained certain results indicating a specific action. Exposure of the whole of the vertebral column of the frog at 90,000,000 cycles per second resulted in all cases in an immediate and strong response, the effect, a violent muscular contraction, being observed in the hind legs. These experiments were repeated with external heat as the agent and the characteristic reaction of leg muscles as observed for high frequency dosage failed to take place.

Besides these experiments in which the vacuum tube was the physical means there are at least two investigations in diathermy which point to effects other than heat—those of D'Arsonval, 1914, and Bennedetti,

1926. D'Arsonval worked with irradiated toxin in experiments similar to those of Szymanowski. Bennedetti treated the seeds of several varieties of common garden plants. He used a Rumkorff coil and spark excitation, making his exposures in a combined electromagnetic and electrostatic field. Treated seeds, he found, germinated and grew more rapidly than controls. Treatment raised the temperature of the seeds about $\frac{1}{2}$ degree centigrade, and, in order to compensate for this factor, he kept all controls at the temperature of the radiated seeds for the duration of the exposure. His results led him to conclude that the small temperature rise due to the field of exposure was not the cause of the favorable germination and growth-rate in treated seeds. McKinley, 1930, using the vacuum tube oscillator treated the seeds of Golden Bantam corn and obtained a slight acceleration in the early germination period, but these experiments have not yet been correlated with the heat factor.

THE PRODUCTION OF SYNTHETIC FEVERS

Carpenter and Page, 1930, taking advantage of the very quick and certain heating effect of exposure to the high frequency field were able to obtain synthetic fevers in animals, including man, without the injection of foreign substances. They followed the suggestion of Hosmer, 1928, who had studied heating effects on salt solutions of various concentrations and on small laboratory animals, and have contributed a therapeutic agent of very great possibilities. By proceeding cautiously they were able to treat 25 human patients, obtaining fevers of 104 to 105 degrees fahrenheit in 60 to 80 minutes. The patient was suspended in the field so that the waves oscillated through the body from one side to the other; the head was not exposed. They were careful to use

the lowest possible current and seem to have avoided entirely all the skin and muscle blistering found by Hosmer and by MacCreight and McKinley, 1930, to accompany hard dosage. All of their patients showed no ill effects, complaining only of slight nausea or headache during exposure.

Carpenter is convinced that in spite of the crudities of the present day apparatus this method of obtaining artificial fevers is not only practical but efficient and will prove of great value to the clinician, physiologist, biochemist and bacteriologist. He also studied the relation of this synthetic fever to infectious diseases in laboratory animals and believes that two desirable effects are obtained by raising the body temperature. First, the increased heat within the body makes a less favorable environment for the multiplication of virus. Second, the heat increases the rate of those chemical processes concerned with the development of immunity and with the general defense mechanism of the body against infectious agents.

The investigation of artificial fevers has been taken up by several medical centers in the United States and Canada, but especially at the University of Rochester under the direction of Carpenter, J. R. Murlin and S. L. Warren. Unpublished results indicate that high frequency oscillations may be an effective agent in the control of such diseases as paresis, gonococcal arthritis and syphilis. Experimentation along this line has been carried on with human patients, and the preponderance of favorable results has encouraged the investigators to continue.

Schliephake, 1928, '29, investigated lethal effects on mice and various insects in connection with a nervous hypersensitivity, finding that brain tissue has the highest heating rate, and he, with others, believes that high frequencies are more or

less specific for nervous tissue. Headlee and Burdette, 1929, found for insects that the nervous reaction speeds up the rate of producing internal heat; the more specialized the nervous tissue the greater the increase in speed of reaction. Of many organic chemical compounds which they measured they found that cholesterol, which is characteristic of nervous tissue, had the most rapid heating rate. McKinley, treating holometabolous insects, where there is a marked difference between the nervous organization of the larva and the adult, found that the lethal time of the larva was about six times that of the adult. In hemimetabolous forms, where there is little difference in the nervous organization of the nymph and adult, the lethal time was about the same.

Schliephake made careful studies of comparisons of heating rates in diathermy and the modern high frequency oscillator. He found that in diathermy the greater heating effect is in fatty tissues. In the high frequency condenser field the heating was found to be more evenly distributed in all the tissues. His experiments showed that the modern condenser field as compared to diathermy has a much greater depth of action.

Exact comparisons between the condenser field and diathermy, or comparisons of the effects of various frequencies, are very difficult at the present moment. For this reason development of methods to measure accurately the output between the exposure plates is eagerly awaited. Until he has this measurement the investigator has little more than an opinion to offer when he speaks of the differential action of various wave-lengths. Scherschewsky believes they are distinctly selective; Christie and Loomis doubt the possibility. Schliephake was led by his experiments to conclude that a change in wave-length brings about a change

in rate of heating of various tissues. Baldwin and Nelson, 1929, however, after work on histological preparations of tissue from rats killed by high frequencies concluded that there was no selective action.

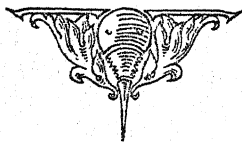
It is perhaps probable, as pointed out by Schereschewsky, that the wave-lengths now being used are too far removed from any possible natural period of body cells or cell aggregates. This natural tissue wave-length, which he estimates to lie between 0.5 and 3 or 4 millimeters, is, as has been stated, beyond the possibilities of the present day vacuum tube. Such a


wave-length lies very close to the near infra-red and the lowest wave-length yet secured with the vacuum tube is about 40 centimeters. We might say, then, that the utility of the three electrode vacuum tube in biology has already been well established, but that it is, nevertheless, still a rather crude instrument. Much of this crudeness will no doubt be corrected within the next few years; and it may even be that the physicists will give us a tube with which we may reach these hypothetical tissue frequencies—with which we may perhaps, treat some one body organ without in any way affecting the others.

LIST OF LITERATURE

- BALDWIN, W. M., and NELSON, W. C. 1929. Histological effects produced in albino rats by high frequency currents. *Pro. Soc. Exp. Biol. and Med.*, Vol. 26, pp. 588.
- BENNEDETTI, E. 1926. Intorno all'azione del campo elettromagnetico oscillante ad alta frequenza su alcuni germi vegetali. *Atti R. Accad. Naz. Lincei. Rend. Cl. Sci. Fis. Mat. e Nat.*, 4 (7/8), pp. 324-332.
- CARPENTER, C. M., and PAGE, A. B. 1930. Production of fever in man by short radio waves. *Science*, Vol. LXXI, No. 1844, pp. 450-454.
- CHRISTIE, R. V., and LOOMIS, A. L. 1929. The relationship of frequency to physiological effects. *Jour. of Exp. Med.*, Vol. xlix, No. 2, p. 302.
- D'ARSONVAL, A. 1914. *Arch. d'Electr. Méd.*
- GOSSET, A., GUTMANN, A., LAKHOSKY, G., and MAGROU, I. 1924. Essai de therapeutique du "cancer experimental" des plantes. *Comptes Rend. de la Soc. de Biol.*, Vol. 91, p. 626-628.
- HEADLEE, T. J., and BURDETTE, R. C. 1929. Some facts relative to the effect of high frequency radio waves on insect activity. *Jour. N. Y. Ent. Soc.*, Vol. 37, No. 1, pp. 59-64.
- HUXFORD, W. S. 1925. Standing waves on parallel wires. *Physical Review*, Corning, N. Y., 2nd series, Vol. 25, pp. 686-695.
- HORLACHER, W. R. 1930. An attempt to produce mutations by the use of electricity. *Science*, Vol. LXXII, No. 1856, pp. 96-97.
- HOSMER, H. R. 1928. Heating effects observed in a high frequency static field. *Science*, Vol. LXVIII, No. 1762, pp. 325-327.
- KAHLER, H., CHALKLEY, H. W., and VOEGTLIN, C. 1929. The nature of the effect of a high frequency electric field upon paramoecium. *Public Health Reports*, Vol. 44, No. 7, pp. 339-347.
- MACCREIGHT, J., and MCKINLEY, G. M. 1930. Biological effect of temperature variations with high frequency oscillations. *Pro. Soc. Exp. Biol. and Med.*, xxvii, pp. 841-843.
- MCKINLEY, J. G., and MCKINLEY, G. M. 1930. High frequency equipment for biological experimentation. *Science*, Vol. LXXI, No. 1846, pp. 508-510.
- MCKINLEY, G. M., and CHARLES, D. R. 1930. Certain biological effects of high frequency fields. *Science*, Vol. LXXI, No. 1845, p. 490.
- MCKINLEY, G. M. 1930. Some biological effects of high frequency electrostatic fields. *Pro. Penna. Acad. Sc.*, Vol. 4.
- MELLON, R. R., SZYMANOWSKI, W. T., and HICKS, R. A. 1930. An effect of short electric waves on diphtheria toxin independent of the heat factor. *Science*, Vol. LXXII, No. 1859, pp. 174-175.
- NASSET, E. S., and WARREN, S. L. 1930. Some metabolic changes occurring in prolonged diathermy treatments. *Pro. Soc. Exp. Biol. and Med.*, Vol. xxvii, No. 9, pp. 943-944.
- PIERCE, G. W. Piezoelectric crystal resonators and crystal oscillators applied to the precision calibration of wave meters. *Pro. Amer. Acad. Arts and Sc.*, Vol. 59, No. 4.
- SAYERS, R. R. 1927. Review of literature on physiological effects of abnormal temperatures and humidities. *Pub. Health Rep.*, Vol. 42, No. 14, pp. 933-996.

- SCHERESCHEWSKY, J. W. 1926. The physiological effects of currents of very high frequency. Pub. Health Rep., Vol. 41, No. 37, pp. 1939-1963.
- . 1928. The action of currents of very high frequency upon tissue cells—upon a transplantable mouse sarcoma. Pub. Health Rep., Vol. 43, No. 16, pp. 927-939.
- SCHERESCHEWSKY, J. W., and ANDERVONT, H. B. 1928. The action of currents of very high frequency upon tissue cells—upon a transplantable fowl sarcoma. Pub. Health Rep., Vol. 43, No. 16, pp. 940-945.
- SCHLIEPHAKE, E. 1928. Die biologische Wärmewirkung im elektrischen Hochfrequenzfeld. Verhandl. Deutsch. Congr. f. innere Medizin, XL. Kongress, 307.
- . 1929. Tiefenwirkungen im Organismus durch kurze electrische Wellen, I. und II. Teil. Ztschr. Exper. Med., 66, 212 u. 230.
- . 1929. Über die Möglichkeit gesundheitlicher Schädigungen durch elektr. Wellen. Gesundheits-Ingenieur, Heft 46.
- UNDERHILL, C. R. 1930. Electronics in surgery—the radio knife. Electronics, Vol. 1, No. 7, pp. 316-319.





THE PROBLEM OF COLOR VISION IN FISHES

By LUCIEN H. WARNER

White Plains, N. Y.

THE PREFERENCE METHOD

EVIDENCE on color vision in fishes is conflicting. Because of the fact that certain fishes rather consistently respond either positively or negatively to light, it has seemed convenient to certain experimenters to use the preference method in the investigation of color vision in these animals. If it could be shown that a fish, repeatedly forced to choose between two lights differing in wave-length only, always or nearly always selected the same one of these lights (position and other variables being controlled), it would seem impossible to deny that the animal was capable of differential response to wave-length. It should be said at once that no investigator has presented conclusive evidence for such behavior. None has satisfactorily controlled the intensity factor. Even Hess, who has taken more pains than have many others, failed at this point.

Graber (19) was perhaps the earliest investigator to use the preference method in an attack on this problem. He found with the fresh water fishes, *Cobitus barbatula* and *Alburnus spectabilis*, a preference for the dark rather than the light, for blue without ultraviolet rather than blue with ultraviolet, for red rather than green and for green rather than blue with ultraviolet. The following year (20) he obtained about the same results on the marine forms *Gasterosteus spinchia* L. and *Syngnathus acus* L. Furthermore he found that it was possible to reverse the pref-

erence for red over blue by using an intensity of the former twenty times as great as that of the latter. Although Graber's work appears to indicate wave-length discrimination it cannot be accepted as anything more than a suggestion because of technical flaws. The colors were produced by pigmented glass and the intensities were "equated" by using pairs of colors which appeared to be equally bright to the human eye. The source of illumination is not given. Graber described the distribution of the fishes thirty minutes after the beginning of the light stimulation conditions. Hess (25) criticizes him for not also reporting the immediate responses.

The work of Bauer

Bauer (2), using the preference method, came to the conclusion that fish and man differed but little with respect to color vision. The apparatus used was a narrow "phototaxis basin" painted black on all sides but one. This basin, containing the fishes, was placed within a black box, one side of which (that corresponding to the clear glass side of the basin) contained openings into which two filters could be fastened, each extending over one half of that side. The filters were of gelatine, paper or glass and the wave length for each was noted. On the side opposite the filters was a hole for the use of the observer. The light intensity was regulated by moving the source of the light (not described) back and forth. To avoid heat from the light an intervening "water box"

was employed. Bauer also used spectral lights in a part of his work. *Charax punctatus* Gm., *Atherina hepsetus* L., and *Mugil* sp. were used. If unfiltered light (white?) was thrown into one half of the basin, the other half being dark, neither positive nor negative phototaxis was shown. The fishes swam back and forth into and out of the lighted part of the basin. A positive response was given, however, to change of almost any kind. If a piece of white paper were placed at the open side they assembled at that point. They again assembled when the paper was removed or replaced by another. However, if the intensity of the light was made very strong the fishes rushed to the darker part of the basin. The above behavior was found in both photopic and scotopic animals. When photopic fishes were tested with colored lights, using an intensity too low to arouse negative responses, strongly positive movements were observed in the case of blue, green and light yellow. Red light called forth immediate and violent negative reactions. When spectral lights were used, starting from the violet end of the spectrum and gradually increasing the wave-length, this negative reaction was first definitely observed at 610 $m\mu$. In the tests described but one part of the basin was illuminated at a time, the other half being dark. If the two halves of the basin were illuminated by different colors, one of which was red, the fishes in the red half gave pronounced negative reactions to the source of light until they happened to get into the other half when they at once reacted positively. Once in this light they never returned to the red. Bauer did not control the intensity factor directly but maintained that this differential behavior was not due to intensity differences since, when the two halves of the basin were illuminated by white light of different intensities, the animals swam back and forth from one to the other, indifferently.

Further evidence of color vision is offered by Bauer using *Box salpa* L. This species is positively phototactic to a marked degree. When a piece of frosted glass was placed in the filter frame and then, in addition, a piece of blue glass placed over one half of the frosted glass, the fishes assembled in the blue half. Since, Bauer says, the blue half must be darker than the other half, the response is contrary to the normal positive phototaxis and must therefore be determined by color rather than by intensity.

Bauer's general conclusion is that photopic fishes can distinguish differences in wave-length; that scotopic fishes may or may not be able to make such a discrimination.

The work of Hess

Hess has so frequently reported studies using the preference method that detailed consideration cannot be given each. In his best application of the method the light from a Nernst globe was passed through a prism and the resultant spectrum thrown against the side of an aquarium. All other light was excluded. Within the aquarium were usually a large number of young fishes, as many as sixty in some cases. The distribution of these fishes in terms of the percentage which congregated in the various parts of the spectrum was noted. It seems that it would have been better to have used a longer and narrower tank than that used by Hess (27 by 18 cm.) in order to keep more uniform the extent to which the light was transmitted through the water before reaching the various fishes. A wide variety of fishes, both marine and fresh water, were studied. It should be noted that Hess does not report results for all of the species used since some of them (young brook trout, eels, pike and "*Sai-blungen*") did not give "sufficiently useful results." Just what determined whether

a result was useful or not is unknown. Hess used young fishes almost entirely, doubtless because their behavior was more uniform. For this he has been criticized by Reeves (39), a criticism based on Shaffer's work (46) which seems to indicate that the retinal cones of young fishes and of older fishes are quite different.

Hess reports that the majority of the fishes gather in that part of the spectrum

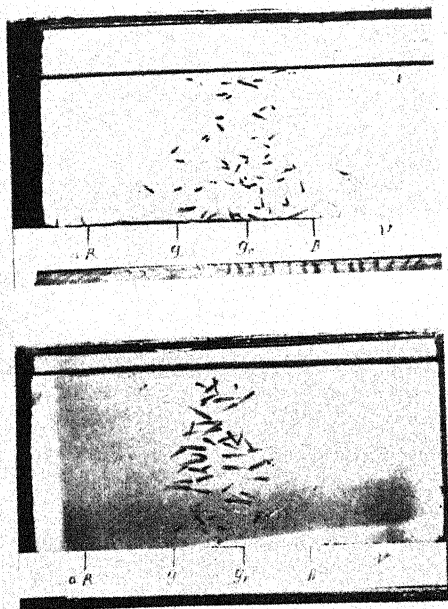


FIG. 1. TWO PHOTOGRAPHS FROM HESS SHOWING CONCENTRATION OF YOUNG FISHES IN THE YELLOW-GREEN PORTION OF A SPECTRUM

bounded by the Fraunhofer lines E and b (that is wave-lengths of 525 to 535 $m\mu$) (Fig. 1). Light of this wave-length would be described by man as green to yellow-green. Since with various intensities of white light these fishes always responded positively to the brightest, it might be said that for them this region of the spectrum appeared the brightest. Not all of the fishes remained in this part of the spectrum. Toward the red end they thin-

ned out rapidly; toward the violet end, not so rapidly. It has been said above that Hess did not control the intensity factor. He appeared not to recognize the fact that a prism does not transmit, with the same amount of loss, light of different wave-lengths. Prisms of different materials vary in the relative efficiency with which they transmit light of various wave-lengths. Unless the characteristic of the prism used is known, and this factor compensated for in some way, different parts of the spectrum thrown by it from a single source of light cannot be known or expected to possess the same intensities. Were we to waive this criticism and accept Hess's assumption that all parts of the spectrum were of uniform intensity we would suppose at first sight that his data indicated color discrimination. To Hess, however, just the opposite is indicated. To him the uneven distribution of the fishes does not represent color preference. Rather, it shows that the brightness value of equally intense lights of different wave-lengths is not the same. A yellow light, for example, has a greater stimulation value than a blue of equal intensity. We assume, perhaps, that each is seen as a gray, but that these grays differ in shade.

In further experiments fishes were tested in a tank lighted not by a spectral band but by two lights, a control light from a Nernst lamp and a monochromatic light obtained by using a very restricted part of the spectrum. The control light was so arranged that its intensity could be varied by the adjustment of its distance from the tank. By keeping the prism and its source of light at a constant distance from the tank Hess expected to be able to produce monochromatic lights of any wave-length desired but always of the same intensity. (But see criticism above.) Starting with the spectral green (lines E to b) lighting one half of the tank he so

adjusted the intensity of the control light thrown into the other half that the fishes distributed themselves uniformly throughout the tank. Under these conditions he presumed that the brightness value of the control light was equal to that of the spectral green. The distance separating the control light from the tank was then taken as unity. The spectral rays were so shifted that first one and then another section took the place of the E-b portion. For each color the control lamp was readjusted, nearer or farther from the tank, until a uniform distribution of the fishes

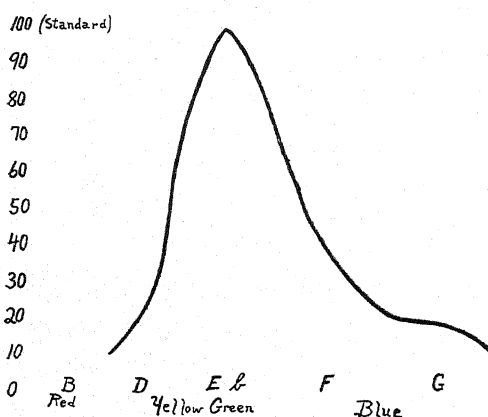


FIG. 2. THIS CURVE, BASED UPON DATA FROM HESS ON YOUNG FISHES, INDICATES THE BRIGHTNESS VALUES FOR LIGHT OF DIFFERENT WAVE-LENGTHS

was again obtained. The distance in each case was noted and expressed in terms of its relation to the distance necessary to obtain uniform distribution for the spectral green. The accompanying graph (Fig. 2) constructed from his data indicates the character of the results. It will be noted that the green or yellowish green portion of the spectrum has the highest brightness value. As the wave-length is increased from this point the value falls off rapidly, becoming zero in the red end of the spectrum. As the wave-length is decreased from this high point the reduction in brightness value is more gradual.

Verification of a sort is to be found in another of Hess's experiments in which each of the two halves of the tank was lighted by a monochromatic light of (supposedly) the same intensity. In general the fishes gathered in that color which, as measured by the method described above, possessed the highest brightness value.

The point which Hess emphasizes continually is that this curve of brightness-values for different regions of the spectrum corresponds rather closely to such curves constructed by Hering for the totally color-blind and the dark-adapted human eye. All three curves are generally similar in shape and have their peaks in the yellow-green region. Hess anticipated the criticism that he obtained such a curve because of the Purkinje phenomenon; i.e., that if brighter lights had been used the peak would have been displaced to the left and the curve might have resembled that for the normal human eye. If this were true his theory would fall. Apparently as a rebuttal he performed an experiment which seems to indicate clearly that when fishes are tested in a dark room immediately after removal from bright daylight an intense light is required to arouse the positive phototactic response; that 45 seconds later a much dimmer light will suffice; that 15-20 minutes later a light having but 1/1000 the intensity of the original light will arouse the response. It is difficult to see why he considered the demonstration of the similarity of the fish and the human eye with respect to darkness adaptation a reply to the criticism that his results would hold only for the degree of brightness he used. His only "proof" lies in the statement that "I could show that within a wide range of absolute light intensities the sensibility of my fishes for differences in brightness is obviously similar to or the same as ours, so

that the higher light intensities—for us—can not have a relatively lesser stimulation value for the fish, which disproves the aforementioned possibility [that the curve obtained holds for only a limited intensity range].”

More recently (30) Hess has reported further experiments relating to these problems but in general they do not differ essentially from his earlier work either in their execution or in the conclusions drawn from them.

A further similarity between response to color in fishes and in the totally color-blind human claimed by Hess is that in

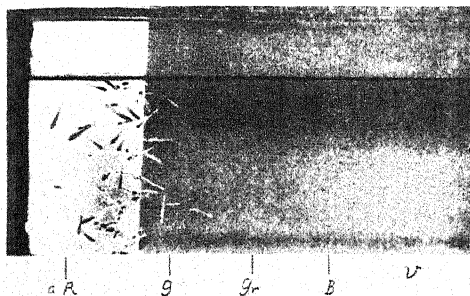


FIG. 3. PHOTOGRAPH FROM HESS SHOWING YOUNG WHITEFISH BEING DRIVEN TOWARD THE RED BY THE GRADUAL CUTTING OFF OF THE SPECTRAL LIGHT BEGINNING AT THE VIOLET END

both cases there is a shortening of the red end of the spectrum. He states that a fish simply fails to respond in any way to light of this quality. In one case in which the tank was illuminated by the entire visible spectrum he commenced cutting off the light, beginning at the violet end. The animals, being positively phototropic, left the darkened part finally being all driven up to the orange portion, all shorter wave-lengths having been eliminated (Fig. 3). As the process was continued they even congregated in longer wave-lengths (620 to 640 $m\mu$) but when only wave-lengths of 650 and over remained the animals distributed themselves evenly throughout the

aquarium just as they would if all light were cut off. Bauer (2), however, failed to verify these results. He found that photopic fishes gathered in darkness in preference to red light (680-710 $m\mu$) and that scotopic fishes gathered in the red light in preference to darkness.

One of Hess's experiments (25) upon the sensitivity of the fish-eye to red is so simple in its execution that it is surprising others have not attempted to verify it. In a dark room the aquarium was illuminated by a Nernst lamp in front of which a red glass was held. A wriggling worm was then thrown into the basin. The fishes paid no attention to this food even though the worm was clearly visible to the experimenter. When the red glass was replaced by a blue one, appearing much darker to the human eye, the worm was at once seized and eaten. Incidentally this experiment indicates that for the species used (not mentioned) visual stimulation was more important than olfactory in the food-seeking behavior of the animals.

Using *Mugil sp.*, a positively phototactic form, Bauer offers evidence that the Purkinje phenomenon occurs in fishes. Photopic animals were given the choice of green or blue, the intensities being so adjusted that the fishes assembled in the green half. Reduction of the intensity (supposedly equivalent for the two colors) reversed the preference, the fishes then gathering in the blue half. Hess criticized Bauer for using green and blue for testing the animals for the Purkinje phenomenon, saying he should have used the customary red and blue. Bauer's reply was that he could not use red because of the "red-fear" which he had found in photopic fishes.

Hess claims that the differential behavior of photopic and scotopic fishes is quite unlike the Purkinje phenomenon and that the latter cannot be demonstrated. He holds that in light-adaptation there is a

pigment, interspersed between the rods and cones and having the power to absorb the shorter wave-lengths. This so arranges itself that it intercepts and absorbs a large part of these wave-lengths before they strike the retinal elements. During dark-adaptation this pigment recedes in such a way as to be much less effective. If, then, the intensities of two lights, one red and one blue, were so adjusted that for the dark-adapted fish (positively phototactic) an indifferent distribution in both halves of the basin were attained, then light-adapted fishes would gather almost exclusively in the red half (since in such fishes the pigment would reduce the efficacy of the blue). In one rather neat experiment which seems to demonstrate clearly the distinction between the Purkinje phenomenon and the effect of dark and light adaptation, dark-adapted fishes were given the choice of red and blue, both lights being of very low intensity. To the experimenter's eye both surfaces appeared almost colorless, the blue being much brighter than the red. The fishes gathered in the blue half. Then, by removing a shutter and moving the sources of light nearer, the intensity of the two colors was greatly increased. To the experimenter's eye (being subject to the Purkinje phenomenon) the red now appeared much brighter. But the fishes still remained in the blue part. Hess states that the characteristics of dark-adaptation persist for a minute or so. After that, supposedly, light adaptation sets in, the pigment becomes effective in reducing the efficacy of the blue and the fishes may approach the red. In a further experiment the blue and red were equalized for dark-adapted fishes at an extremely low intensity. No increase of intensity (equal for both colors) could disturb the uniform distribution of the fishes. Hess's point is, then, that the Purkinje effect is observed

immediately upon the change in intensity of the spectral colors and before the elapse of the minute or more required for adaptation. This immediate shift in the relative brightness values does not occur in fishes. What has been mistaken for this phenomenon (the relative reduction of the efficacy of the shorter wave-lengths with increased illumination) is not the result of the increased intensity of the spectral colors, as such. Rather it is the result of the pigment migration accompanying or constituting the adaptation to any change in general illumination. The fact that this adaptation requires an appreciable lapse of time enables one to differentiate between the two phenomena.

For light-adapted fishes Hess found the yellow-green to green portion of the spectrum to be the brightest. The degree of intensity necessary to equate any other color with pure yellow was only about half of that necessary to equate that color with yellowish green. With the spectral lights, the intensity necessary to equate pure blue with a constant yellowish red was four times as great for light-adapted as for dark-adapted fishes.

It is to be expected that the results reported by Bauer (and others) and by Hess would not be in agreement even though all made use of the preference method. Several possible explanations for the conflicting results are obvious. Only two of these will be mentioned, and these largely because they are in themselves problems of considerable theoretical importance. First, the best evidence for color discrimination that Bauer offered, was in the case of photopic fishes. Most of Hess's observations, on the other hand, seem to have been on scotopic animals although it is true that he makes general remarks to the effect that photopic animals react similarly. Bauer holds that under the two extremes of adaptation fishes react quite differently,

especially to the longer wave-lengths. Secondly, both Hess and his opponents assume that a phototaxis furnishes a form of motivation which can be relied upon to be consistent in strength and direction from individual to individual within a given species, and from one time to another for an individual. Perhaps the reconciliation of the conflicting results which have been reported is to be found not in flaws of technique (though these exist in abundance) but in the assumption that these taxes are flexible and that there are many factors, internal and external, which may alter their degree and even their direction.

A brief summary of Hess's work will be given at this point although other of his studies must be mentioned in later sections. First will be listed criticisms which may be advanced against his studies:

1. He does not seem to recognize the possibility that response to intensity, even though it may dominate response to color, does not necessarily exclude the possibility of the latter.

2. He fails to explain certain inconsistencies in his results. For example, in his 1912 article (25) certain results lead him to the general statement that scotopic fishes react to the spectrum exactly as do photopic fishes. This is not reconciled with his theory of pigment migration dealt with in the same article, nor with the data reported in defense of this theory. Nor does it agree with results reported in other articles as in 1914 (29) where he found that photopic fishes swam to the yellow-green region more quickly and with fewer exceptions than did scotopic fishes.

3. He fails to recognize certain results reported by Bauer (2) and to answer objections raised by this writer against his work.

4. He excludes "unsatisfactory results" (25).

5. He fails to make control tests with normally negatively phototropic fishes.

6. There are a number of sources of error all of which may have been controlled but probably were not since no mention is made of the control:—

- a. Stimulus error. (1) Intensity of light may have varied in different parts of the spectrum because of characteristics of the refracting medium. (2) Thermal cues. (3) Cues from any of the other modalities.

- b. Emotional disturbance following movement of fishes from light to dark.

- c. Effect of water on the light (variability in amount of water through which light passes before reaching eye of the fish).

Hess's work does seem to indicate that the following statements hold for those species used (all positively phototropic):

1. That response to intensity exists, that it probably dominates response to color if fishes are sensitive to color.

2. That the behavior previously interpreted as indicating the Purkinje phenomenon need not be so interpreted.

3. That those forms of behavior described by Bauer and others as "red-shyness" and "love for blue" do not necessarily indicate color vision since such behavior can be reversed by appropriate manipulation of the intensity factor.

Hess's work has had an important influence in the field of color vision. Parsons (37), for example, states that in his opinion the adverse criticism levelled against Hess has not seriously shaken his position. In our opinion, Hess's greatest contribution was that of calling attention to the difficulty of establishing evidence for color-discrimination and especially to the danger of interpreting brightness-discrimination as color-discrimination.

THE LEARNING METHOD

The learning method has been used even more frequently than the preference

method. Unfortunately, in a large number of investigations the intensity factor has not been controlled (5) (13) (41) (52). Washburn and Bentley (49) made an effort to control this factor. One small fish (*Semotilus atromaculatus*) was trained to take food from red forceps and not from green forceps. The two forceps were always presented simultaneously. The red was for the human (light-adapted?) eye the darker of the two colors. After the association had been established, a red, which by the same criterion was lighter, was substituted without interfering with the habit. As Parsons and others have pointed out, it should not be inferred that the brightness values for colors are the same from one group of animals to another. To be sure that the brightness values of any pair of colors had been reversed, it would be necessary to vary both of them within extremes too great to be obtained by daylight reflected from a pigmented surface.

The practise of varying the intensity of one or both stimuli, keeping the wavelengths constant, has been employed by practically all investigators in their efforts to determine whether differential response has been based on the intensity or the wave-length characteristics of the stimuli. Application of this principle is found in the work of Reeves (39), Schiemenz (43), and others. Goldsmith (18) has employed another method of equating her stimuli for brightness, but one which is faulty. She photographed her colored surfaces and finding that some of them photographed a darker gray than others she attempted to compensate for this by using filters of varying thickness. This method involves the unwarranted assumption that the intensity values of different wave-lengths are the same for the eye of the fish as for the photographic plate.

Reighard (40) noted that gray snappers (*Lutianus griseus*) preferred white bait to

blue and blue bait to red. When these were to the human eye matched with grays on color wheels the brightnesses were in the order white, red and blue. Since the choice in one case favored the brighter and in the other the less bright bait, he assumed this choice to have been based upon color. In further experiments he fastened *Cassiopea* tentacles to baits stained various colors in order negatively to condition the fishes to such colors. The fishes came to refuse harmless bait stained the same color as those previously bearing the tentacles. Varying the brightness of the stains did not seem to affect the behavior of the animals (i.e., if negatively conditioned to red they refused bait stained all shades of red, although they accepted bait of other colors). Reighard concluded that these fishes were capable of color discrimination. Obviously the range of intensities procurable by this method would be limited.

Hess (25) rejects as worthless the work of Zolotnitzky, of Reighard and of Washburn and Bentley on the grounds of unsatisfactory intensity control. To show that brightness was indeed the criterion of discrimination he carried out the following experiments. Minnows and Mugil were fed red chironomus larvae. Then, colored threads of the size and shape of the larvae were glued to the outside of the basin. The fishes disregarded the yellow and white decoys and snapped at the red. This is just what Zolotnitzky found. But Hess went further and tested the animals on various shades of gray, blue and green and was able to find a shade of each to which they responded just as regularly as they did to the red. In further experiments he used imitation larvae made of various chromatic and achromatic papers pasted against paper backgrounds. He was able to produce decoys which were responded to positively when against a dull

white or light gray background. When such a decoy was pasted against a bright red background it was apparently not reacted to at all. When against a pure (?) yellow background there was fastened a decoy of blue paper of a certain brightness the fishes failed to react, although for the human eye the blue differed in hue very distinctly from the yellow background. When against this background a blue decoy of a different brightness was pasted the fishes snapped vigorously. These results are in distinct contradiction to those of other investigators.

Further feeding experiments of Hess (29) served only to strengthen his faith in his previous conclusions. About that time, however, Bauer and Degner (4), using the same general method, came to the conclusion that fish have color vision, though only when they are light-adapted.

The work of von Frisch

Von Frisch (13) repeated certain of Hess's experiments, failing to confirm the latter's results. *Phoxinus laevis* which had been fed for a long time on yellow colored meat snapped at decoys of yellow paper against a gray background. If, as Hess maintained, they snap only at objects which show brightness contrast then a given gray should be found which would have the same brightness value as the yellow decoy pasted upon it at which the fishes would not snap. Von Frisch used a long series of graded grays and did not find one which caused the fishes to refrain from snapping at the yellow decoy. After the fishes had been fed red colored meat for a time they were offered, on a gray background, a small piece of red and a similar piece of black paper. They invariably snapped at the red, never at the black. The same thing happened when the background was black or dark gray. Von Frisch says that this is not the be-

havior we would expect in an animal whose vision resembled that of the color-blind human. Fishes trained to red would snap at red and at yellow decoys, but not at any other color. Fishes trained to yellow behaved similarly. Both types of fishes snapped at purplish red and both snapped occasionally at greenish yellow but almost never at blue-green or blue.

In further experiments von Frisch used a large number of 8 cm. glass test tubes lined with papers of various colors and with papers of a series of fifty grays ranging from black to white. Shot was placed in the bottoms of the tubes so that they would rest on the bottom of the tank. For a given group of fishes (*Phoxinus*, usually six tested at a time) six gray tubes and one colored tube were used. Only the colored tube contained food, the others being empty. After several weeks of training the fishes always went directly to the colored tube, irrespective of its position, avoiding the grays. They did this even though the colored tube contained no food. The whole series of grays was used and in no case did a fish confuse any shade of gray with the color to which it had been trained. Then, instead of gray tubes each group was given the choice of red, yellow, green, blue and purple-red tubes in an effort to determine which colors were confused. It was found that red and yellow were quite regularly confused but that blue and green were distinguished from each other and from yellow or red. Purple-red was also confused with red and with yellow. Tabulated numerical results support these conclusions fairly well (a feature the more appreciated since it is infrequently encountered in these studies). Von Frisch holds that these results explain (1) the widespread occurrence of red as a decorative color and (2) the fact of undifferentiated adaptation to red and to yellow backgrounds in *Phoxinus*.

Burkamp (6) has more recently tested various Cyprinides including Phoxinus in much the same way using, instead of test tubes, trays of various colors and of twenty-four intensities of gray (Fig. 4). The animals were tested in groups of six to twelve. The data, which are reported in tabular form, seem to indicate that the fishes learned to respond positively to the tray in which they had always found food, avoiding, usually, trays of other colors. The trays were so designed as to conceal the food until the fish had definitely made

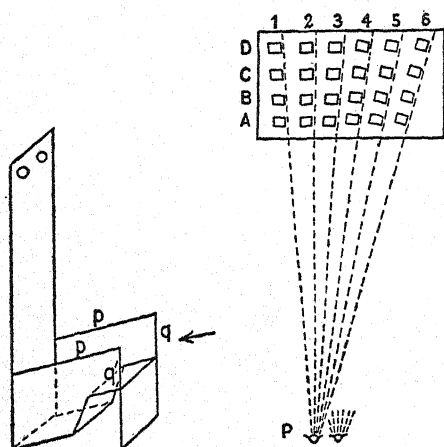


FIG. 4. AT THE LEFT IS SHOWN ONE OF THE TRAYS USED BY BURKAMP. A FISH COULD NOT SEE INTO THE TRAY UNTIL IT SWAM DIRECTLY OVER IT. AT THE RIGHT IS SHOWN THE ARRANGEMENT OF THE TWENTY-FOUR TRAYS

a selection. The position factor was controlled. Intensity was partially controlled by using a confusion series of grays, one of which was supposed (for the fish) to be equivalent in brightness value to the color in question. Olfactory control was apparently attained by using food in none of the trays in the test series although this is not clearly stated. The results, in general, support the findings of von Frisch.

The work of White

White (50) has studied the mudminnow (*Umbra limi*) and the stickleback (*Eucalia*

inconstans) using light from a 10-watt Mazda lamp transmitted through gelatine light filters allowing only a narrow band of the spectrum to pass. The fishes were offered food under one color and an unpalatable substance under another. A fish which consistently reacted positively toward a substance offered under the light beneath which it was accustomed to receive food, and negatively under the other light was supposed to have discriminated between the two. Variation in intensity of the light (1.4 to 4.9 c.m.) did not affect the discrimination. Experiments with various shades of gray showed but poor discrimination ability and consequently White is inclined to believe that wavelength difference was the determining factor. The mudminnows apparently distinguished between red and green, red and blue, and yellow and green. The sticklebacks were successful on only the first pair. Realizing that this control of intensity was hardly more adequate than that of previous investigators, she repeated her work (31), using only mudminnows. The following filters were used: red, 660–700 m μ ; yellow, 560–600 m μ ; green, 510–550 m μ ; blue, 400–450 m μ . She states that "the total radiant energy transmitted by these filters was equalized to within about 5 per cent by the addition of layers of neutral-tint film." Unfortunately, we are not informed how these measurements were made, i.e., whether radiometric or photometric methods were used. Furthermore, the range of 5 per cent is not a small one. Otherwise her experimental technique resembled that of her former experiment. She found differential response to the following pairs of colors: red and green, red and blue, red and yellow, yellow and blue. There was no evidence for discrimination between blue and green.

Even were we to grant that White's control of intensity was adequate (that the

lights of the two wave-lengths radiated the same amount of energy), it is quite unlikely that the results reported would persuade Hess that the fishes responded to color. Differential response to differences in wave-length and differential response to color are not necessarily the same. The former involves the factor of luminosity, which varies with variation in wave-length even though intensity remains constant. The latter, supposedly, does not involve this factor. The method used in the studies of White is capable of yielding data on the former problem only. Thus the titles of her articles are misleading.

The work of Reeves

There is a method which can yield data on the latter problem (color discrimination) if we are justified in making the assumption that correction for variation in luminosity can be made by appropriate regulation of the intensities of the lights. Reeves (39), a student of Reighard, has applied it to the study of fishes. The apparatus was essentially a Yerkes-Watson discrimination box modified so that it could contain water. The source of light was a Nernst lamp. Red and blue filters restricted the transmitted light to but a portion of the spectrum. Variation of intensity was produced by the adjustment of the width of a slit placed between the lamp and the filter.

Glass filters transmitting each of the following colors were used: red (572 to 652 $m\mu$), and blue (509 $m\mu$ to the end of the visible spectrum). An adjustable slit placed between the lamp and filter furnished the means of altering the intensity. Food was presented for correct choices by means of a mechanical device. In every case the animals were trained toward the blue, the intensity of which was kept constant throughout the work. The red light was varied in intensity "so as to

include an intensity equal to the blue." At what intensity of the red its luminosity would be equal to that of the blue for the eye of the fish was of course unknown. The supposition would have to be that by using a very wide range of intensities this intensity would be included. According to the procedure used by Reeves the red was at its maximum during the training series. After the positive response to the blue and the negative response to the red had been fairly well established, the intensity of the red light was gradually decreased. The animal was still fed only before the blue. If the differential behavior of the fish to the two lights were on the basis of color we might expect it to continue in spite of intensity variation. If this behavior were established on the basis of intensity difference it would be expected that at some point the luminosity factor for the red and the blue would be equated for the eye of the fish and the discrimination would break down. If the fish could not respond differentially to color, as such, no amount of training at this point could result in any but a chance distribution of choices for the two lights. In this experiment Reeves used four horned dace (*Semotilus atromaculatus*, Mitchell) and three sunfishes (*Eupomotis gibbosus* Linnaeus). In the case of every subject eighteen correct choices out of a series of twenty were made for at least one degree of red intensity. It thus seems that an association involving discrimination between the two lights was formed in every case, whatever were the characteristics of the stimuli which determined the behavior. There is a surprising lack of uniformity in the records of the various fishes. There was in every case considerable variation in the percentage of correct choices as the intensity of the red light was reduced but this variation was different from fish to fish. We would expect

that within a given species there would be but little variation in the intensity of a red light of the same luminosity as the standard blue light. This did not seem to be the case. The intensity of the red light is indicated only in the width of the slit in mm. In the case of one horned dace the number of correct choices, which had been as high as nineteen out of twenty with a width of 35 mm. (the maximum intensity), dropped to thirteen out of twenty at 0.9 mm. With another dace the low point (ten out of twenty) was reached with 5.0 mm. In the case of the other two dace the percentage correct in a series never dropped below 70. For two of the three sunfish, the low point was reached at 1.8 mm. and at 0.9 mm. respectively. The third sunfish was not given preliminary training at maximum intensity and the results were irregular. But, in spite of these inconsistencies, it may be that the low points do represent failure of the animals to discriminate on the basis of luminosity and that at these points the two lights are equated for this factor. If this is true then we have the ideal situation for the determination of the ability of the animals to discriminate color. It is merely necessary to continue training with these two lights so equated for luminosity. If a discrimination can be established it must be on the basis of color difference.

For some reason this was done with but four of the seven fishes and in three of these cases but one additional series of twenty trials was given at the point where the discrimination broke down. Nevertheless, these few data are of crucial importance, being the only data of their sort in the literature on color vision in fishes. Semotilus "Md," made 13 correct choices out of the first 20 with an intensity of 0.9. Of the next 20 choices with the same intensity "83%" was said to have been correct (perhaps it is meant that 16 of 19 were

correct). No further detail as to the order of correct and incorrect choices within a series is given. The statistical validity of the difference between these two short series is not sufficient to warrant definite conclusions. In the case of the second dace so tested, "Y1," the difference is negligible (10 correct choices in the first 20 at 5 mm. and 11 correct in the second 20). In the case of one of the two sunfishes so tested the number correct, having dropped to 11 out of 20 at 0.9 mm., rose to 35 out of the next 40. This difference appears to be significant. For the other sunfish the increase is not appreciable, being from 13 to 14 in 20. If we were to accept data secured by this method as proof for or against color vision we would be forced to say that while the evidence is strong for such in the case of one of the sunfish and fair in the case of one of the dace, data for the other two fishes offer just as good evidence against color discrimination. It could be objected that adjusting the intensity of the red in fairly large steps, as was done, might not necessarily result in the securing of an intensity at which the two colors were perfectly equated. The drop in correct choices might indicate merely that the intensity difference had been so reduced as to render an intensity discrimination difficult and that further training at this point raised the level of the fish's performance. Other experiments of Reeves seem to show that intensity differences to be discriminated by fishes must be relatively large. This throws some doubt on the above explanation of her data. According to an entirely different and perhaps the most plausible explanation the cause of the total or partial failure of the discrimination habit which ordinarily followed intensity changes was merely confusion on the part of the fish. This confusion might well be expected as a result of the changes made in the stimulus situa-

tion to which it had been trained. Similarly, ultimate recovery of the habit might be expected to follow an adjustment to change in the situation. This explanation would render it unnecessary to account for the fact that the break-down in the habit did not always occur with the same intensity of the red light.

Reeves' conclusion that "sunfish and horned dace discriminate light of longer wave-length from light of shorter wave-length" should be accepted as merely tentative, pending further data on the problem.

The work of Schiemenz and others

A recent study made by Schiemenz (44) resembles that of Reeves in that he also kept wave-length constant and varied intensity. The learning required of the fishes (*Gasterosteus aculeatus* and *Phoxinus laevis*) was somewhat different, being rather more like that required of the animal in the experiment of Washburn and Bentley (49). The fishes were trained to accept food from a glass rod. The uniformity of presentation of this rod was insured by the use of a mechanical device. In a training series the fishes learned to leap for the food only when it was presented under the illumination of a certain narrow band of spectral light, and not when illuminated by light from other portions of the spectrum. Having set up this differential response the problem was to determine whether it was based upon color or luminosity differences. Schiemenz attempts to solve this problem by wide variation in the intensities of the lights. Twelve degrees of intensity were used. This differed from the method of Reeves in that he did not determine at what relative intensities lights of different wave-lengths possess the same luminosity value for the fish. Instead he hoped to use such a range of intensities that, were the re-

sponses made on the basis of luminosity rather than color, the fishes would sometimes choose one color, and sometimes the other. Schiemenz reports that he succeeded in training these animals so that they responded positively to all intensities of the color associated with food in the training series and to no intensity of any color not in the immediate neighborhood of this color in the spectrum. By testing the animals on colors differing only slightly from the positive color in wave-length he was able to get an approximation of the acuity of the animal at various points on the spectrum. He reports that their acuity at the blue end of the spectrum was slightly superior to that of man, that at the red end it was inferior. In all test series the rod, whether presented with the positive light or with another light, bore no food. All tests were made on light-adapted fishes in diffuse light.

Three studies, one by Kühn (33), one by Wolff (51) and one by Hamburger (22), differ in method from that of Schiemenz chiefly in the fact that the fishes (*Phoxinus laevis* in every case) were presented simultaneously with a number of areas of light, differing in wave-length, and including one under which the fishes had formerly been trained to feed. The fishes learned to leap from the water for food only in the area where they had previously been fed. Like Schiemenz, these investigators varied the intensities and report that differences of wave-length, rather than of intensity, determined the animals' behavior. In general their conclusions are in accord with those of Schiemenz. Hamburger further offers evidence that, to mixtures of two lights of such wave-lengths as to be complementary (appearing white to the human eye), the minnow responds in the same way that it responds to white light.

The fact that Scharrer (42) was unable to train blinded specimens of *Phoxinus* to

discriminate between lights of different wave-length suggests that such discrimination is mediated by the eye.

Although Froloff (17) has recently reported data suggesting that *Tinca vulgaris* can distinguish a red from a green light, it is almost certain that the differentiation was based on intensity difference. Froloff was not primarily interested in color reception and admittedly made no effort to use lights of equal energy.

THE PIGMENT CELLS AND COLOR VISION

A type of behavior which has been claimed by some to demonstrate color vision in fishes is the response of the pigment cells to backgrounds of various colors. Sumner (47) and Mast (36) have reported detailed observations of such behavior in the flounders. Both investigators demonstrated that the essential receptor was the eye. Mast concluded on the basis of his observations that color vision in fishes is essentially the same as it is in man. As in the case of practically all studies of color the intensity factor was uncontrolled and thus on this basis we are forced to say that these observations may be indicative of color vision, but are not proof. Presuming, however, that this criticism be waived, there is, nevertheless, a question as to whether behavior of this type could ever establish color vision. To quote from Washburn (48):

Watson does not think that these observations prove color discrimination in the fish. He says, "Ordinarily, when we say that an animal is sensitive to difference in wave length we mean that such stimuli play a rôle in the adjustment of the animal to food, sexual objects, shelter, escape from enemies, etc.; that such stimuli initiate activity in arcs which end in the striped muscles." Because the changes of color are produced not by such arcs, but by the sympathetic nervous system, Watson thinks color vision not proved: "We can easily conceive," he says, "of mimicry of this kind taking place in an animal whose retina does not contain the physico-chemical sub-

stances necessary to initiate response to differences in wave-length." But since the changes of color are induced by differences in wave-length and induced through the retina, we may reply that it does not seem easy, or in fact at all possible, to conceive of the absence of such photochemical substances from the fish's retina.

Whether or not the behavior in question establishes color discrimination is not a matter that can be proven or disproven. It depends upon how one defines that term.

The work of von Frisch and others

Von Frisch (10), who studied this form of mimicry in *Crenilabrus pavo* and *Trigla corax*, reports that when a fish is transferred from one background to another differing from the former in both intensity and color, it accommodates itself first with respect to brightness and then with respect to color. He says that he was able to find a gray paper which appeared to the minnow to be of the same brightness as a certain yellow (or red) paper, for it would accommodate itself to the same brightness (in its own pigmentation) on both. Nevertheless, when the fish was on the yellow paper, expansion of the yellow pigment cells occurred, while this did not happen when the fish was on the gray paper. In another experiment he used as a background first a yellow and then a blue fluid (evidently as a color filter) which were at first so highly concentrated that they appeared black, and then were gradually diluted until they were practically white. In both cases all degrees of brightness were assumed by the fish but the expansion of the yellow pigment cells occurred only in the case of the yellow fluid.

In another experiment (11) von Frisch procured yellow papers of the same color value but of differing degrees of brightness. When transferred from one to the other, the minnows became decidedly brighter, or darker accordingly. Then a gray paper

was chosen which when interchanged with the lighter yellow caused no difference in the brightness of the fish. This gray was assumed to be equated for brightness value with the lighter yellow. When this gray was substituted for the darker yellow, however, a brightening resulted. The two yellow papers were therefore more different from each other with respect to brightness, than were the gray and the lighter yellow. Nevertheless, after prolonged exposure to either yellow paper, there was always expansion of the yellow pigment cells, whereas on the gray background these consistently contracted.

Von Frisch concludes that the minnow possesses a sense of color and recognizes red and yellow as such and not by their brightness values alone, as Hess seems to think probable. In so far as his observations may be accepted as indications of color vision they indicate but a primitive stage of such ability. These fishes reacted only to red and yellow, and to these colors in almost the same way, apparently showing that they were not received as qualitatively different. Green, blue and violet were accommodated to only with respect to brightness.

Hess subjects von Frisch's earlier work, in which the intensity factor was uncontrolled, to the severest criticism. Hess of course holds that all behavior in fishes, apparently determined by differences in wave-length, is actually determined by differences in intensity. Nevertheless, this writer reports some data which certainly uphold von Frisch's view that color mimicry is determined by wave-length differences. Using gray backgrounds of varying intensity values (photometrically determined) Hess found that *Phoxinus laevis* showed no differences in color whether it was on a dark or a bright background, even though the latter were five times as bright as the former. He had

previously shown, however, that fishes were sensitive to a difference in brightness of 1.23 to 1.00. In spite of this it is his opinion that any color-matching of which fishes may be capable is the result of brightness rather than wave-length discrimination.

Haempel and Kolmer (21) tested *Phoxinus laevis* Ag. and *Cottus gobio* L. using both transmitted and reflected light. They found little evidence for color mimicry except in the case of minnows which had been taken from the river Wuerm, which has a red bottom. These assumed a red tint when placed in an aquarium lined with red paper and did not so respond when paper of gray or of other colors was used. There is no evidence offered, however, to show that this response was not made on the basis of intensity.

Freytag (8) was able to observe mimicry of intensity but not of color in *Phoxinus laevis*. Reeves (39) objects to his negative conclusions regarding color vision on the grounds that he did not allow the animals sufficient time for adaptation to color.

Connolly (7) has studied the adaptive changes of *Fundulus* to backgrounds illuminated by spectral lights of different wave-lengths. The lights used were of equal energy as determined by means of a thermopile and galvanometer. He found that *Fundulus heteroclitus* adapted rather slowly, but that after a week's exposure those animals subjected to yellow and red lights were quite distinct from those subjected to blue.

The contention of Hess, that the changes in the brightness values of colors accompanying adaptation are due to the migration of a retinal pigment, receives support in the work of Schnurmann (45). Both these writers contend that data, which apparently indicate color vision, actually demonstrate the effect of retinal pigment. This yellowish pigment, retracted during

dark-adaptation, spreads over the retinal elements upon exposure to light and acts as a differential filter. They conceive its effect to be much like that of yellow tinted glasses upon a color-blind person. In both cases we would expect a far greater absorption of short than of long wave-lengths.

The work of Schnurmann

Schnurmann's data are too extensive to be cited here. He observed the melanophore reactions of light-adapted fishes (*Phoxinus laevis*) to chromatic backgrounds verifying Hess's conclusions (based on different methods) regarding the relative brightness values of different colors. He then tested the brightness values of various colors on a totally color-blind woman with and without the use of a yellow filter. The results showed absorption of a part of the mixed light (gray) and a still greater absorption of a part of the short wave-lengths by the yellow filter. An interesting counter test would have been measurement of the brightness values in dark-adapted fishes, since in such animals the retinal pigment is retracted and thus non-functional.

If such fishes could be tested both with and without the use of a filter of yellow glass, further evidence might be obtained in support of the analogy in function between the glass filter and the retinal pigment. Such tests were impossible, however, since light-adaptation occurred more rapidly than did the melanophore response.

That the retinal pigment seemed to exert no effect in the decoy tests (24) is explained by the fact that those rays which enter the eye at right angles to the back surface of the retina (in other words, those which come from a small object which is fixated,) are not absorbed by the pigment because of its peculiar structure.

Schnurmann makes this statement con-

cerning the reactions of the chromatic pigment cells in *Phoxinus*: "During three and one half month's investigation on minnows from the Ulmar region, I was unable to discover any yellow coloration on yellow, red or orange backgrounds which I could not also get on differently colored or achromatic background of all degrees of intensity." These fishes assumed a yellow coloration in darkness which they lost upon increase in illumination.

The fishes from the Munich region, on the other hand, regularly became yellow over yellow, orange and, to a lesser extent, red backgrounds. The latent time of yellow matching was much longer than that of brightness matching, requiring from one-half hour to five hours. Disappearance of the yellow coloration was just as slow. In deep basins the yellow coloration usually did not occur. Supposedly this was because the effect of the yellow ground was not continuous on the dorsal side of the retina. The matching was only relative, not absolute, the coloration being the same whether the background was yellow, 120 degrees, or orange, 37 degrees. The same fishes which became yellow on a yellow background (those from the Munich region) also became yellow if held in an absolutely or very nearly dark place. The three conditions under which the xanthophores expanded, therefore, were:—

1. Absolute darkness (no rays for the yellow pigment to absorb).
2. Very weak light (the yellow pigment being retracted, absorbed but few rays).
3. Yellow or reddish-yellow background (the yellow pigment having few rays to absorb inasmuch as the background reflected only long-waved rays. This refers to the dorsal retina only).

In short, when the pigment of the dorsal retina is absorbing light of short wave-length the yellow pigment of the skin con-

tracts. When the pigment of the dorsal retina is not absorbing such light, the yellow pigment of the skin expands. Thus there may be a reflex connection between the retinal pigment, in its activity or non-activity, and the pigment cells of the skin. This separation of the reflex connections governing brightness-matching from those governing color-matching, corresponds with the differences in latent time, if we imagine that it requires some time for the chemical changes in the retinal pigment to take place.

There is another conception of this matter of matching, which would account for the behavior of *Phoxinus* without implying color vision. Melanophore contraction is determined by equalization of the amount of light striking the retina in all its parts. We would get brightening, therefore, in complete darkness, in deep water where the axis of the retina is being continuously changed, and on light backgrounds which reflect most of the light striking them. Expansion of the melanophores occurs when the dorsal retina does not receive the same amount of light as the ventral or lateral retina. Xanthophore contraction, on the other hand, is determined by non-equal illumination of the various parts of the retina. On a blue background, for instance, the dorsal retina is exposed mostly to short wave-lengths which are to a great extent absorbed by the retinal pigment. On a red or yellow background practically none of the rays reflected from the bottom to the dorsal retina are absorbed whereas the short waves coming from above are absorbed. Thus equalization of stimulation causes xanthophoric expansion. So in darkness or near darkness there is equalization and yellow coloration.

Schnurmann's observations and interpretations are important, not merely in themselves, but because they stress the

fact that there may be an adequate explanation of the matching of chromatic backgrounds which does not involve the assumption of color vision.

OTHER EVIDENCE

Hess has made a study of another unlearned response as it is related to stimulation by colored light. The pupil of the eye of most fishes responds to an increase in intensity of illumination by contraction. Hess has recorded these responses both by photography (25) and by means of a measuring device, the pupilloscope (30). By this means he has obtained data concerning the relative brightness values of light from different parts of the spectrum but of (supposedly) equal intensity. He asserts that the results obtained corroborate his other work, indicating that these brightness values are the same for fishes as for the totally color-blind human eye.

A form of evidence, or rather argument, that has been used for and against the existence of color vision in fishes relates to the utility of such ability should it exist. Hess maintains that monochromatic light, especially of the longer wave-lengths, penetrates the water to such a short distance that in most cases there would be no colors for fishes to see even though they had color vision. Von Aufsess (1) has shown that in 8 meters of water (from Bavarian lakes) only $1/60$ of the red waves ($600\text{ m}\mu$) is still present. At a depth of 20 meters only $1/10,000$ remains. Hess himself made experiments on this problem using Hering colors. The papers were protected against water by celluloid. At a depth of 2 meters, in bright daylight the red looked a dull brown; at 3.6 meters the orange looked brownish yellow though the yellow and blue could still be recognized clearly; at 4.6 the red and orange could not be seen as such but as gray;

at 5.6 meters none of the colors could be recognized. One sample of each color was tested against a black and one against a white background. The following question still remains open: Is it merely the depth of water through which the light passes downward that destroys certain of the wave-lengths and thus renders the colors invisible, or is not also the quantity of water through which the colored paper is seen a factor? Our interest is in the way these papers might look to the fishes. Hess should have observed their appearance with his eye submerged to their level. But even though it could be conclusively demonstrated that monochromatic light did not penetrate to any great extent into the normal environment of a fish, this would not be proof that the animal was color-blind. There are other forms of stimulation, not normally found in the environment of many animals, which, nevertheless, when presented, are effective stimuli.

In support of color vision, the point has been made that the coloration acquired by fishes during the mating season must have developed for a "purpose" which could not be fulfilled if the fishes were color-blind. Von Frisch names a number of fishes which

breed at night or at such depths that color would be invisible. All of these fail to acquire bright hues during the mating season. He also gives a list of species which, mating under conditions where color would be visible, acquire such coloration. Hess notes one exception to this correspondence of coloration and habit (the Saiblinge). This is not sufficient grounds, according to von Frisch, for rejecting the evidence of the other thirty-odd species.

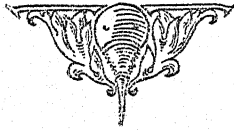
Consideration of the many and conflicting data on the subject has led the writer to conclude that some fishes, at least, do respond to color as such. Anglers, with their kits of flies of all hues, would scoff at any other conclusion. It is very probable, however, that the capacity to discriminate colors is far less developed in some species than in others. There may also be age differences. Nine-tenths of the experimental work in the field would bear repeating. Especially the investigations of Hess, which have often yielded data out of harmony with most other workers, should be repeated carefully. Many of his techniques are most ingenious and should furnish admirable starting points for truly conclusive experimentation.

LIST OF LITERATURE

- (1) AUFSCH, O. v. u. z. 1913. Seeing under water, how things look from a fish's point of view; abstracted by the Berlin correspondent of the Scientific American from Deutsche Alpenzeitung, Jan., 1913. Scient. Amer., 108: 469-70.
- (2) BAUER, V. 1910. Ueber das Farbensecheidungsvermögen der Fische. Pflügers Arch., 133: 7-26.
- (3) ——. 1911. Zu meinen Versuchen über das Farbensecheidungsvermögen der Fische. Pflügers Arch., 137: 622-6.
- (4) BAUER, V., und DEGNER, E. 1913. Über die allgemein-physiologische Grundlage des Farbenwechsels bei dekapoden Krebsen. Z. allg. Physiol., 15: 363-412.
- (5) BULL, H. O. 1928. Studies on conditioned responses in fishes. Part 1. J. Mar. Biol. Ass. U. K., n.s., 15: 485-533.
- (6) BURKAMP, W. 1923. Versuche über das Farbenwiedererkennen der Fische. Z. Psychol. Physiol. Sinnesorg., Abt. II. Z. Sinnesphysiol., 55: 133-70.
- (7) CONNOLLY, C. J. 1925. Adaptive changes in shade and color of Fundulus. Biol. Bull., 48: 56-77.
- (8) FREYTAG, G. V. 1914. Lichtsinnuntersuchungen bei Tieren. Arch. vergl. Ophthalm., 4: 151-61.
- (9) FRISCH, K. VON. 1912. Färbung und Farbensinn der Tiere. Sitzber. Ges. Morph. Physiol. München, 28: 30-8.

- (10) FRISCH, K. VON. 1912. Über farbige Anpassung bei Fischen. Zool. Jahrb., Abt. Zool. Physiol., 32: 171-230.
- (11) —. 1912. Sind die Fische farbenblind? Zool. Jahrb., Abt. Zool. Physiol., 33: 107-26.
- (12) —. 1912. Über die Farbenanpassung des Crenilabrus. Zool. Jahrb., Abt. Zool. Physiol., 33: 151-64.
- (13) —. 1913. Weitere Untersuchungen über den Farbensinn der Fische. Zool. Jahrb., Abt. Zool. Physiol., 34: 43-68.
- (14) —. 1923. Das Problem des tierischen Farbensinnes. Naturwissenschaften, 11: 470-6.
- (15) —. 1925. Farbensinn der Fische und Duplizitätstheorie. Z. wiss. Biol., Abt. C. Z. vergl. Physiol., 2: 393-452.
- (16) FRÖLICH, A. 1913. Vergleichende Untersuchungen über den Licht- und Farbensinn. Deuts. med. Wschr., 30: 1453.
- (17) FROLOFF, J. P. 1928. Bedingte Reflexe bei Fischen. Pflügers Arch., 220: 339-49.
- (18) GOLDSMITH, M. 1914. Réactions physiologiques et psychiques des poissons. Bull. Inst. gén. psychol., 14: 97-239.
- (19) GRABER, V. 1884. Grundlinien zur Erforschung des Helligkeits- und Farbensinnes der Tiere. Prag, Tempsky, 322 p.
- (20) —. 1885. Ueber die Helligkeits- und Farbenempfindlichkeit einiger Meertiere. Sitzber. Akad. Wiss. Wien., math.-naturw. Kl., Abt. I., 91: 129-50.
- (21) HAEMPEL, C., und KOLMER, W. 1914. Ein Beitrag zur Helligkeits- und Farbenanpassung bei Fischen. Biol. Zbl., 34: 450-8.
- (22) HAMBURGER, V. 1926. Versuche über Komplementär-farben bei Ellritzen (*Phoxinus laevis*). Z. wiss. Biol., Abt. C., Z. vergl. Physiol., 4: 286-304.
- (23) HESS, C. 1910. Ueber den angeblichen Nachweis von Farbensinn bei Fischen. Pflügers Arch., 134: 1-14.
- (24) —. 1911. Experimentelle Untersuchungen zur vergleichenden Physiologie des Gesichtssinnes. Pflügers Arch., 142: 405-46.
- (25) —. 1912. Vergleichende Physiologie des Gesichtssinnes. Jena, Fischer, 299 p. (Reprinted from Bd. 4 of the Handbook of Comparative Physiology. Ed. by Hans Winterstein.)
- (26) —. 1913. Über die Entwicklung von Lichtsinn und Farbensinn in der Tierreihe. Verh. Ges. deuts. Naturf. Aerzt. 1913 (Ersterteil): 127-47.
- (27) —. 1913. Untersuchungen zur Frage nach dem Vorkommen von Farbensinn bei Fischen. Zool. Jahrb. Abt. Zool. Physiol. 31: 629-46.
- (28) HESS, C. 1914. Über die Entwicklung von Lichtsinn und Farbensinn in der Tierreihe. Wiesbaden, Bergmann, 33 p.
- (29) —. 1914. Untersuchungen zur Physiologie des Gesichtssinnes der Fische. Z. Biol., 63: 245-74.
- (30) —. 1919. Über Gesichtsfeld Silberglanz und Schqualitäten der Fische und über die Lichtverteilung im Wasser. Z. Biol., 70: 9-40.
- (31) HINELINE, G. M. W. 1927. Color vision in the mudminnow. J. Exp. Zool., 47: 85-94.
- (32) KRAUSE, W. 1897. Die Farbenempfindung der Amphioxus. Zool. Anz., 20: 513-15.
- (33) KÜHN, A. 1925. Versuche über das Unterscheidungsvermögen der Bienen und der Fische für Spektrallichter. Nachr. Ges. Wiss. Göttingen, 1924: 66-71.
- (34) KURZ, F. 1920. Versuche über den Einfluss farbigen Lichtes auf die Entwicklung und Veränderung der Pigmente bei den Fischen. Zool. Jahrb., Abt. Zool. Physiol., 37: 239-78.
- (35) LONGLEY, W. H. 1917. Studies upon the biological significance of animal coloration I. The colors and color changes of West Indian reef-fishes. J. Exp. Zool., 23: 533-97.
- (36) MAST, S. O. 1916. Changes in shape, color and pattern in fishes and their bearing on the problems of adaptation and behavior, with especial reference to the flounders, *Paralichthys* and *Ancylopsetta*. Bull. U. S. Bur. Fish., 34: 173-238.
- (37) PARSONS, J. H. 1924. An Introduction to the Study of Color Vision. Cambridge, England, Cambridge University Press, 157 p.
- (38) POLIMENTI, O. 1916. Sur le sens chromatique des poissons recherché au moyen de réactions dans le rythme respiratoire. Arch. ital. Biol., 64: 300-5.
- (39) REEVES, C. D. 1919. Discrimination of light of different wave-lengths by fish. Behav. Monog., 4: No. 19, 106 p.
- (40) REIGHARD, J. E. 1908. An experimental field-study of warning coloration in coral-reef fishes. Carn. Instn. Pub. 103: 257-325.
- (41) SCHALLER, A. 1926. Sinnesphysiologische und psychologische Untersuchungen an Wasserkäfern und Fischen. Z. wiss. Biol., Abt. C, Z. vergl. Physiol., 4: 370-464.
- (42) SCHARER, E. 1928. Die Lichtempfindlichkeit blinder Ellritzen. (Untersuchungen über das Zwischenhirn der Fische I.) Z. wiss. Biol., Abt. C., Z. vergl. Physiol., 7: 1-38.
- (43) SCHIEMENZ, F. 1924. Ueber den Farbensinn der Fische. Z. wiss. Biol., Abt. C., Z. vergl. Physiol., 1: 175-220.

- (44) SCHIEMENZ, F. 1927. Das Verhalten de Fischer in Kreisströmungen und in geraden Strömungen, als Beitrag zur Orientierung der Fische in der freien natürlichen Wasserströmung. Z. wiss. Biol., Abt. C., Z. vergl. Physiol., 6: 731-50.
- (45) SCHNURMANN, F. 1920. Untersuchungen an Elritzen über Farbenwechsel und Lichtsinn der Fische. Z. Biol., 71: 69-98.
- (46) SHAFER, G. D. 1900. The mosaic of the single and twin cones in the retina of *Micropterus salmoides*. Arch. Entw. Mech. Org., 10: 685-91.
- (47) SUMNER, F. B. 1911. The adjustment of flatfish to various backgrounds. A study of adaptive color change. J. Exp. Zool., 10: 409-506.
- (48) WASHBURN, M. F. 1908. The Animal Mind. 3rd. ed. 1926. New York, Macmillan, 431 p.
- (49) WASHBURN, M. F., and BENTLEY, I. M. 1906. The establishment of an association involving color-discrimination in the creek chub, *Semotilus atromaculatus*. J. Comp. Neurol., 16: 113-25.
- (50) WHITE, G. M. 1919. Association and color discrimination in mudminnows and sticklebacks. J. Exp. Zool., 27: 443-98.
- (51) WOLFF, H. 1925. Das Farbenunterscheidungsvermögen der Elritze. Z. wiss. Biol., Abt. C., Z. vergl. Physiol., 3: 279-329.
- (52) ZOLOTNITSKY, N. 1901. Les poissons distinguent-ils les couleurs? Arch. Zool. exp. gén., 33, 9: 721-5.





NEW BIOLOGICAL BOOKS

The aim of this department is to give the reader brief indications of the character, the content, and the value of new books in the various fields of biology. In addition there will frequently appear one longer critical review of a book of special significance. Authors and publishers of biological books should bear in mind that THE QUARTERLY REVIEW OF BIOLOGY can notice in this department only such books as come to the office of the editor. The absence of a book, therefore, from the following and subsequent lists only means that we have not received it. All material for notice in this department should be addressed to Dr. Raymond Pearl, Editor of THE QUARTERLY REVIEW OF BIOLOGY, 1901 East Madison Street, Baltimore, Maryland, U. S. A.

BRIEF NOTICES

EVOLUTION

THE FORMENKREIS THEORY AND THE PROGRESS OF THE ORGANIC WORLD. *The Re-Casting of the Theory of Descent and Race-Study to Prepare the Way for a Harmonious Conception of the Universal Reality.*

By O. Kleinschmidt. Translated by the Rev. F. C. R. Jourdain. H. F. and G. Witherby
10s. 6d. net $5\frac{1}{2} \times 8\frac{3}{4}$; 192 London

This is a distinctly disappointing book. After a careful reading, we remain unable to give any clear statement either of the meaning the author attaches to the term *Formenkreis* or to the theory itself. As far as we have been able to make out, the *Formenkreis* is a taxonomic unit used by the author in preference to the genus or the species; but there is nothing in the way of a clear statement of just what determines his classification, and how it differs from that of other taxonomists. As regards his theory, the case is a little clearer. He appears to hold that the *Formenkreis* is the largest unit within which relationship by descent can be shown to hold. He denies that one *Formenkreis* can arise from another; and while he is a trifle vague on the point, he

seems to lean toward the independent origin of different forms.

Whether there is any great merit in the author's ideas we cannot say; because, as already indicated, we are still in the dark as to just what these ideas are.



RATIONAL EVOLUTION (*The Making of Humanity*)

By Robert Briffault The Macmillan Co.
\$3.50 $5\frac{3}{4} \times 8\frac{1}{2}$; 302 New York

A book for your pastor, if he can read. The author dislikes Christianity considerably, and argues with much plausibility that Arabic culture was the real source of modern culture. We suspect that he overestimates the Arabs, as we are sure that he underrates Aristotle. But with all the statements which the reader will regard as erroneous or doubtful, the book is well worth reading.



ADAPTIVE MODIFICATIONS IN THE WOODPECKERS. *University of California Publications in Zoology, Volume 32, No. 8.*

By William H. Burr
University of California Press
\$1.00 $7 \times 10\frac{3}{4}$; 70 (paper) Berkeley

A detailed anatomical account of the

modifications of the skeletal and muscular systems of the various species of woodpeckers, which are regarded as adaptations of their habits of life.

The adaptive modifications in the various structures such as the tail feathers, pygostyle, or skull show a positive correlation with the habits of the birds. This correlation is repeated many times in the group, and because of its recurrence the evidence is strengthened for considering that the environment, likely, at least in part, through natural selection, has been an important factor in modeling the group as we see it today.



GENETICS

A NEW THEORY OF HEREDITY

By *George A. Gaskell* C. W. Daniel Co.
2s. 6d. 4 x 6½; 93 London

The theory advanced in this book seems, so far as we know, to be new; whether it is true is another question. A few quotations will allow our readers to judge for themselves:

The Discovery of the actual method of the mental and vital transmission of influence for the production of organisms. First, there is the contacting of the psychic nature with the physical, resulting in the formation of a mass of watery and nutritive 'living matter' in which bioplasts are endued with sensation, desire and hunger, and thereby *guided* mentally in the use of physical forces and particles of matter required in the construction of organisms. The microscope reveals the process.

Notwithstanding the general belief in parental heredity, no evidence can be found for it. Such evidence as there is relating to conception and the process of growth, directly contradicts the idea of inheritance coming from or through parents. Proof of the transmission by parents to offspring of acquired or any other characteristics is entirely wanting.

A warmed hen's egg may produce a chicken in an incubator after its parents have been killed and eaten, which shows that parents have nothing whatever to do with the heredity of their species.

A swan or albatross must use up enormous power in flying, yet the muscles of its wings are not torn, although the bird may be for hours in the upper air. This source of force we may anticipate will become

accessible to human beings when man investigates his own mental and psychic nature guided by a *true* theory of life, free from the misleading errors of the present variety of authoritative theories.

This force, which may be called provisionally 'etheric force,' would be very welcome for aeronautics, and its accessibility is likely to be accomplished in no great length of time by the application of psycho-mental methods of research into the causes of normal and abnormal phenomena of life and mind, and the relation these phenomena must have to heat, electricity and currents in the ether.



THE LABORATORY MOUSE. *Its Origin, Heredity, and Culture.*

By *Clyde E. Keeler*

Harvard University Press

\$1.50 6 x 9; viii + 81 Cambridge

A brief and attractive summary of data on the mouse, with particular reference to its use as material for genetic experiments. There are chapters on the geographical distribution of the house mouse, on the antiquity of the fancy mouse, on unit characters, on normal and on abnormal inheritance, on laboratory breeding, and a bibliography of 184 titles.



L'HÉRÉDITÉ. *Deuxième Édition, Revue et Augmentée.*

By *Émile Guyénot*

G. Doin et Cie

32 francs

Paris

4½ x 7; vi + 470 (paper)

This is one of the best accounts of the present state of our knowledge of genetics which has come to our attention. The exposition is clear and logical, the choice of examples excellent, and the documentation ample.



GENERAL BIOLOGY

JORULLO. *The History of the Volcano of Jorullo and the Reclamation of the Devastated District by Animals and Plants.*

By Hans Gadow
\$3.00 (U. S. A.)
7s. 6d. (England)

The Macmillan Co.
New York
Cambridge University Press
Cambridge

5 $\frac{3}{8}$ x 8 $\frac{1}{2}$; xviii + 100

The eruption which built up the volcano of Jorullo in Mexico, began in 1759 and continued intermittently for several years. Prior to this time not only had there been no sign of volcanic activity but the region, an area of about fifty square miles, had been one of great fertility. In fact, the name Jorullo, meaning Paradise, had been given to the district. With the series of eruptions, an area of at least five square miles was completely buried in mud, sand, and lava, while a much larger area suffered widespread destruction of plant and animal life. Ashes fell as far as 125 miles distant. Within 90 years of the catastrophe the flora had practically regained the lost ground, except in those places where the lava covered the surface.

Gadow visited the region in 1908. At that time he found every available stretch of level ground, except the Malpais (lava fields) under cultivation. The slope of the volcano was densely wooded, although as late as 1872, the vegetation reached scarcely half way up and was very thin. The author deals with the story of the eruption as it has been recorded by various individuals and the history of the invasion of the devastated region by plant and animal life as he found it. He found that animal life was restricted almost entirely to reptiles and amphibia. Even so, considerable exploring of the unaffected region was necessary to trace the lines of invasion. The work includes a map showing the geological formation of the volcano and the surrounding region. Philip Lake contributes an editorial preface and there is a prefatory note by A. C. Seward.

THE INTERPRETATION OF DEVELOPMENT AND HEREDITY. *A Study in Biological Method.*

By E. S. Russell Oxford University Press
\$5.00 5 $\frac{3}{8}$ x 8 $\frac{1}{2}$; 312 New York

In this interesting book Dr. Russell begins with a historical sketch of theories of development and heredity from Aristotle to the present day, and then develops a theory of his own, to which he applies Ritter's name 'organismal.' This emphasizes the functional unity of the living thing. While analysis is a necessary process in science, it always leaves something out of the picture. He is therefore critical of particulate theories, such as that of the gene. The evidence that the nucleus alone determines development and heredity is defective. Rather the evidence is that the nucleus and cytoplasm interact in the process.

The book is well worth reading. If it does not convince the particulatist of the error of his ways, at least he will profit by this critique of his foundations.



DAS LEBENSPROBLEM *im Lichte der modernen Forschung.*

By O. Kestner, L. Rhumbler, J. von Uexküll, L. Weickmann und P. Mildner, G. Wolff, R. Woltereck. Edited by Hans Driesch with Foreword by Heinz Woltereck.

Quelle und Meyer

20 marks 6 $\frac{3}{4}$ x 9 $\frac{3}{4}$; xi + 461 Leipzig

This collection of essays deals with the origin, the nature, and the conditions of life. It is written with true German *Gründlichkeit*; for instance, Professor Kestner's article on The Functions of Life would serve very well as an introductory text on physiology. In the last article Professor Driesch rehearses his reasons for concluding that the individual must be identified with the entelechy.

PHILOSOPHY OF A BIOLOGIST

By Sir Leonard Hill

Longmans, Green and Co.

\$1.40 $4\frac{1}{2} \times 7$; viii + 88 New York

In this readable little book a distinguished physiologist gives us his synthesis of modern science. That the physiological section of the book is the most colorful and interesting is perhaps natural. His summing up is

that modern science has brought us to the conception of a power eternal, infinite, unknowable, "the power behind the sun" of the Egyptian king Akhnaton, energizing all in the universe, the dead no less than the quick; a power equivalent to the purest conception of God stripped of all dogma and superstition; a power in all and through all, whence we came, of which we are a part, and whither we return after death; a power active in all atoms of matter composing the nebulae, the stars, the dust and the living cell; a power determining every action and reaction in the eternal evolution of the universe, the earth and life upon earth. The mystery of a living cell is, then, neither less nor greater than that of a drop of water; ceaseless reactions to the environment occur in both. The author suggests, too, that the recent developments of neurology, such as the study of reflex actions by Sherrington and conditioned reflexes by Pavlov, by lifting the veil which has hung over the reactions of the nervous system, are becoming of fundamental importance in the guidance of education.

Science, having dispelled the superstitions of past ages, should keep us to a pure faith and free from any modern revivals of witchcraft. The great conjurers have never been excelled by the manifestations of spiritualists, and the supposed messages of those who have passed over are characterized by a triviality which corresponds with the intellects of charlatans who act as mediums. Such a book as the *Road to Endor* was of great service in showing how clever men confessedly tricked a whole community by methods which lead the credulous to belief in spiritualism.

While metaphysics, creeds, spiritualism, remain barren, the exact observations and operations of scientific research, applied, not to war at the behest of ignorant governments, but to peace, work wonders in saving life and extending happiness.



A SURVEY OF NATIONAL TRENDS IN BIOLOGY

By Edward J. v.K. Menge

The Bruce Publishing Co.

\$2.00 $5\frac{1}{2} \times 7\frac{5}{8}$; xi + 156 Milwaukee

A set of lectures prepared for the National University of Cordoba (Argentina), dealing with the outstanding biological theories and workers of the present time.



HUMAN BIOLOGY

TABLEAUX D'HISTOIRE GÉNÉRALE.

Présentation Synchronique des Principaux Événements Contemporains à travers les Siècles. Politique, Religions, Philosophies, Lettres, Arts, Sciences, Découvertes, Inventions, Institutions.

By J. Berthier and C. Lauvernier

Société Mercasia

160 francs net

Paris

 $10\frac{3}{4} \times 14\frac{1}{4}$; 43 double page tables

+ 6 pages index

Chronological outlines of history are among the most useful of all reference books. Such a work is the equivalent of a digest of the daily newspapers as they appeared (or would have appeared if there had been any) day by day since the beginning of records. This is the form in which any sensible man wants the record presented. Historians have almost invariably confused and befuddled the common man (and irritated the scientifically minded man as well) because they have felt it imperative in their manner of presenting the subject to depart from the newspaper's simple chronological record of what happened day by day.

The present volume is extremely well done. A double page is devoted to a century of time, beginning with 600 B. C. and ending with 1900 A.D. On such a double page is recorded, against a horizontal time scale, the flow of events in the fields of politics, religion, philosophy,

letters, arts, sciences, and other human oddments. In the later centuries, where one double page is not enough to take care of all these classes, the century is reduplicated as many times as necessary until all subdivisions have been adequately treated. The result is superb. There is naturally somewhat heavy emphasis upon French events and personalities, but after all the French have been and are a highly important branch of mankind—perhaps the most highly civilized human beings yet evolved—and any possible overemphasis of their achievements in this volume is not at the expense of other peoples.

We recommend this book unreservedly to our readers.



WILLIAM STEWART HALSTED.

Surgeon.

By W. G. MacCallum

The Johns Hopkins Press

\$2.75 5½ x 8½; xvii + 241 Baltimore

The old saying that genius is an infinite capacity for taking pains is nowhere truer than in the case of the great surgeon. But this is only half the story. We all know people who take infinite pains over their work and yet produce a hopelessly mediocre result. The genius has the further gift of knowing what to take pains over and what kind of pains to take. These two qualities of fertility of mind and meticulous attention to detail were strikingly exemplified in Dr. Halsted. In his biography Dr. MacCallum has drawn a vivid picture both of the great surgeon and of the elusive but intriguing personality. Perhaps the best summing up of Halsted as a surgeon is that which he quotes from Leriche.

For those who have visited the Johns Hopkins Hospital, two things stand out: Halsted has created

a method in surgery and he has inspired disciples. It is this that gives his clinic such vivid originality, and when one has seen intimately that admirable organization one understands why Baltimore has rapidly become the cradle of contemporary surgery in the United States.

The method of Halsted rests primarily on the biological idea, for those in Baltimore are the surgical inheritors of the spirit of Claude Bernard. It is taught there that surgery should be above all an experimental science. It is on experiment that surgical pathology should lean constantly if it is to progress, and on the other hand experiment should precede and follow every new operative attempt. Surgery is only applied biology . . . In Baltimore the fusion of surgery and physiology is intimate. The education of the students is above all biological, and the future surgeons are trained in a laboratory of experimental surgery in contact with living beings, and not in a dissecting room.

Halsted has established the principle that the surgical operation, to attain all that can be expected of it, should respect life, not only of the individual but of the tissues. It must not introduce the least infection and must not traumatise the tissues. On the other hand nothing in the operation can be left to chance. There can be nothing approximate in experimental biology, and every operation should be a physiological experiment in which the desired result should be obtained with mathematical exactness.



THE BOOK OF MY LIFE. (*De Vita Propria Liber*)

By Jerome Cardan. Translated from the Latin by Jean Stoner

E. P. Dutton and Co., Inc.

\$3.50 5½ x 8; xviii + 331 New York

Cardan was a genius, beyond question. He had many of the accepted *stigmata*. No one can doubt this who reads Henry Morley's delightful biography. As is not uncommonly the case with superior men Cardan excessively irritated lesser persons, not only contemporaneously but in perpetuity. He had to wait a long time before a really sympathetic biographer appeared in the person of Henry Morley. Now, three quarters of a century after the appearance of Morley's life, there appears to be a considerable re-

awakening of interest in old *Girolamo*, of which the present volume is an evidence. What this is due to is not easy to say—perhaps the New Humanism is responsible in part, and perhaps the present widespread interest in biography plays a part.

In any case, whatever the reason, it is good to have this fresh translation of Cardan's most famous book, the *De Vita Propria Liber*, which has never before been published *in toto* in an English version. Morley's characterization of the book is the best possible description of it, as "no autobiography, but rather a garrulous disquisition upon himself written by an old man when his mind was affected by much recent sorrow."

The present translation is an honest, painstaking one, perhaps more remarkable for a rather literal sort of accuracy than for literary grace. Everyone interested in human biology will want to read the book and have it on his shelves for permanent reference. If the publisher and translator want to have blessings (and probably not cash) showered down upon them they will go ahead and bring out a complete translation of Cardan's *Opera Omnia*.

GROWTH OF CHILDREN IN HAWAII;
BASED ON OBSERVATIONS BY LOUIS
R. SULLIVAN. *Memoirs of the Bernice P.
Bishop Museum, Volume XI, Number 2.*
*Bayard Dominick Expedition Publication
Number 17.*

By Clark Wissler

Bernice P. Bishop Museum
Honolulu, Hawaii

\$2.00

$9\frac{1}{2} \times 12\frac{1}{2}$; 151 (paper)

The collection of anthropometric measurements and of data on qualitative characters of the Hawaiians was one phase of the major problem of studying the origin and migration of the Polynesian

people, an investigation carried on by the Bayard Dominick expedition. Dr. L. R. Sullivan had charge of the Hawaiian work. He had completed the task of gathering the material in 1921 but had not put it in usable form before his death occurred. To Dr. Clark Wissler fell the duty of assembling the tabulations for publication and of writing the descriptions and comparative statements. Records were obtained on about 1000 pure Hawaiian adults, 2000 mixed Hawaiian individuals and 9000 school children ranging in years from 5-19 and representing the following groups: Hawaiian, Chinese, Japanese, North European, South European, Korean, Filipino, Hawaiian-Asiatic, Hawaiian-North European, Hawaiian-South European, and Hawaiian-Asiatic-European.

The report includes descriptions of the measurements taken and 67 tables exhibiting the statistical data collected, and a literature list.



CHILD LABOR IN NEW JERSEY. *Part 3.*
The Working Children of Newark and Paterson.
U. S. Department of Labor, Children's Bureau
Publication No. 199.

By Nettie P. McGill

U. S. Government Printing Office
Washington

15 cents

$5\frac{3}{4} \times 9\frac{1}{8}$; v + 94 (paper)

In this survey of child labor in New Jersey two bulletins have previously appeared on (1) employment of school children and (2) children engaged in industrial home work. The present bulletin, dealing with the cities of Newark and Paterson, gives an exhaustive statistical survey of progress in school, grade completed, and age at date of leaving school, occupation and industry, wages, unemployment, steadiness at work, etc. Among

the results which this study yielded are the following:

Newark and Paterson working children had been younger on going to work and had had less schooling than children in many other cities who go to work before the age of 16. The great majority had less than an elementary-school education.

Discontinuing school and going to work was not associated with the loss of the father in the case of either girls or boys.

The great majority of the children in both cities became semiskilled factory operatives.

The proportion of those who had worked less than a year who could be classified as definitely unsteady was very large, but only a small percentage of the workers in both cities who had been at work as long as a year would be so classified. Children who had been 15 on first going to work seemed to have had a somewhat wider choice of employment, less unemployment on the whole, and slightly better wages, except in the case of Paterson girls, than those who had been younger. Children from the lower grades were more likely to take factory employment, those from the higher grades office and sales work.



RACE MIXTURE. *Studies in Intermarriage and Miscegenation.*

By Edward B. Reuter

Whittlesey House (McGraw-Hill
Book Co., Inc.)

\$2.50 5 $\frac{3}{8}$ x 8; vii + 224 New York

This book consists of a group of papers which have been delivered before sociological societies. Most of them have appeared elsewhere in print. Each paper forms a complete study in itself but they are all on the same general subject, race mixture, and throughout all of them there runs the general thesis that: "The physical differences between races, particularly skin color, is made the basis for caste distinction and differential treatment which give rise to psychological and sociological phenomena that are in no sense racial and may be understood only in social terms."

After a general discussion of civilization and the mixture of races the author devotes

much space to the amalgamation of the black and white race, particularly in this country, and the mental achievements and social status of the product of this mixture. There are chapters on sex distribution in the mulatto population, the legal status of racial intermarriage, the superiority of the mulatto, the hybrid as a sociological type, etc. He recognizes the superior achievement of the hybrid but in the analysis of this superiority finds that it can hardly rest in an improvement due to blood mixture. Rather it lies in the "cultural contacts and personal mobility consequent upon the mixed ethnic origin." The book contains bibliographic references and is indexed.



CHINESE CIVILIZATION

By Marcel Granet Alfred A. Knopf, Inc.

\$7.50 6 x 9 $\frac{1}{4}$; xxiii + 444 New York

The writer has attained a remarkable insight into ancient Chinese civilization from a thorough exploration of original sources. He has presented much more than a documentation of events, for he reveals a rare comprehension of the complex phenomena of social organization in ancient China.

The most interesting chapters of this book are those portraying Chinese "society," in particular the details of public and private life. The keynote of this civilization in its highest development was etiquette.

There is among the Chinese a mastery of their sensibilities that is simply extraordinary. Decorum, etiquette have repressed all spontaneous display and resulted in an at least apparent drying up of feeling. The expression of the emotions—and notably of mourning—has an entirely conventional character.

Public life is one continuous parade governed by the most elaborate rules. Whether or not this is as true for the masses of people it is hard to say, since

little is known. But the history of the upper classes shows that

During the long centuries of its ascendancy the Chinese acquired precious virtues through their feudal discipline. They recognized the merits of formalism, of regulated actions, of ready-made formulas. They understood the moral value of conformity. As an essential duty they laid down the practice of the most entire and genuine loyalty: they had the wisdom to define it by a formal adhesion to a whole collection of consecrated conventions of established hierarchies, of good traditions. They made sincerity and honour the fundamental principles of their conduct and their thought. They codified with strictness the practice of these virtues, and when they decided to devote their lives to the worship of etiquette, they succeeded in avoiding the uneasiness of mind which may result from anarchical pursuit of the just and the true.

In private life also everything is dominated by rules. Conventionalized conduct and respect are substituted for intimacy and affection to a degree that would astound westerners. "Regulated on the model of court assemblies, domestic life forbids all familiarity. Etiquette rules there and not intimacy."

The development of this highly cultivated taste for decorum from the instinctive desires of contest, and "passion for prestige," arouses ones admiration. Thus it happened that battles became highly refined and cultured, where each side refrained from being discourteous to the extent of beating the other badly up. All relations were fixed by custom, and the ideal striven for was one of "strained politeness."

Finally in political life where the stage is reached of advocating the principle of government by history, it appears that it is claimed as sufficient for everything to follow solely the virtues of a traditionalist conformity. So, at the moment when, towards the beginning of the imperial era, Chinese civilization seems to arrive at a point of maturity, everything cooperates to bring to light the reign of formalism.

The author, besides being an historian, is undoubtedly a real artist. He gives

picturesque descriptions of the peasant, his life in the fields, his dwellings, his attire, his habits of life during the various seasons.

Equally good descriptions are given of court life, the feudal lords and family life of the upper classes. Granet's ability to reconstruct this civilization from a tangle of legends, sayings, formulae, songs and records is deserving of great credit.



A TRAVELER IN INDIAN TERRITORY. *The Journal of Ethan Allen Hitchcock, late Major-General in the United States Army.*

Edited and Annotated by Grant Foreman
The Torch Press

\$5.00 6½ x 9½; 270 Cedar Rapids, Iowa

General Ethan Allen Hitchcock, a grandson of the famous Ethan Allen, was a graduate of West Point in 1817. During the Florida wars he distinguished himself by his great tact and fairness in dealing with the Indians. In 1841 he was sent to the Indian Territory to investigate the scandals in connection with the Act which caused the Indian tribes of the east to be removed to the western reservation. Not only was the report of this investigation never allowed to come before Congress, too many friends of the Administration having been involved in the famous transaction, but it disappeared completely from the government files. General Hitchcock kept copious notes, however, not only on his criminal investigations but on all that came within his notice. Domestic scenes, habits and customs of the tribes that he visited, their amusements, quarrels, religious beliefs and tribal councils all interested him. These notes are now published in the form of a journal. Undoubtedly, General Hitchcock did not intend them for publication, at least in their original form, for he included

many details concerning his own movements which could have little interest for the reader. But his records are well worth reading for the vivid picture which they give of Indian life as it existed ninety years ago. In an appendix appear several letters written by General Hitchcock which were discovered by the editor after the journal had gone to press. The work includes a map of the Indian territory and an index.

GENETIC STUDIES OF GENIUS. Volume III. *The Promise of Youth. Follow-up Studies of a Thousand Gifted Children.*

By Barbara S. Burks, Dortha W. Jensen and Lewis M. Terman. Assisted by Alice M. Leaby, Helen Marshall, Melita H. Oden.

Stanford University Press
Stanford University, Calif.

\$6.00

5 $\frac{3}{4}$ x 8 $\frac{5}{8}$; xiv + 508

This volume contains the results of a follow-up study of the gifted children reported on in volume I of these studies. Part I of this volume is devoted to statistical analysis and discussion of the performance of the children on various tests and their achievements thus far in their career. Part II is devoted to case studies, and Part III to a study of juvenile literary production, with an attempt to derive a scale for rating the literary merit of such work.

We were somewhat surprised and perplexed in reading the chapter on the retests of intelligence. It was found that those children who took the Stanford-Binet test, and whose I.Q.'s could consequently be determined showed a lower average I.Q. on retest. The possible reasons for this change are discussed and debated at length; but there is no indication that such a change might be the natural result of an imperfect measuring instrument. It would appear obvious that if we selected a group of high I.Q.'s

on the basis of some test, and then retested by some other test, we should expect a lowering of the mean of the group. But we have found no suggestion of this in the book.



BIRTH REGISTRATION AND BIRTH STATISTICS IN CANADA.

By Robert R. Kuczynski

The Brookings Institution

\$3.00 6 x 9; xii + 219 Washington

A book of interest to the vital statistician. Canada is the only country in the world that can boast of a continuous series of birth records covering three hundred years. This, however, is confined to French Canada and is due to the Catholic clergy who in early colonial times inaugurated a system of registration of births, marriages and deaths. French Canadian records show the highest fecundity that has ever been observed in any country. That fecundity, however, has decreased considerably in recent years. In English-speaking Canada birth registration has been no more satisfactory than it has been in the United States. The author devotes considerable space to a discussion of the struggle which the provincial governments have had with clergymen, physicians, civil officials and parents to secure adequate registration and the efforts that have been made to obtain a unification of vital statistics in the Dominion. Included in the report are many tables dealing with birth statistics and an index.



YOUR CHARACTER FROM YOUR HANDWRITING. *A Guide to the New Graphology.*

By C. Harry Brooks

William Morrow and Co.

\$1.75 5 x 7 $\frac{1}{2}$; 207 New York

Graphology is trying to acquire the

dignity of an exact science like chemistry or physics. The author explains about all this in this little book, which is a brief outline of the more copious work of Robert Saudek, one of the world's leading authorities on graphology. The chief accomplishment of this book, however, is to show that character is only one of a number of equally important factors which make for different types of handwriting. And while there are a number of excellent methods prescribed for judging handwriting, one feels that it is rather futile to put too much confidence in them since there are so many elements concerned which are difficult to determine from observing a script, such as age, sex, writing material, etc.



THE BRONZE AGE.

By V. Gordon Childe The Macmillan Co.
\$3.50 New York

$5\frac{1}{8} \times 7\frac{1}{2}$; xii + 258 + map

A careful study of the prehistoric bronze tools, weapons and ornaments of Western Europe and of the pottery and other remains associated with them. The Bronze Age marked not only an advance in technical knowledge but the beginning of industrial specialization. Any hunter or farmer could make a flint knife or arrow-head in his spare time, but mining, smelting, forging and casting were more complicated arts, whose mysteries were handed down in special guilds. Moreover, the limited distribution of copper and tin ores involved wider and more regular trade relations than had been necessary in the Stone Age. The use of bronze began probably in either Egypt or Sumer and spread thence to Europe. Various cultural groups may be distinguished, but their identification with the racial groups of later times is as yet uncertain.

DISEASE AND THE MAN.

By George Draper The Macmillan Co.
\$4.50 $5\frac{1}{4} \times 8$; xix + 270 New York

A book which should interest a wide circle of readers. It continues along the lines of the author's earlier *Human Constitution*, but also discusses the psychological relations of constitution and disease. The facts presented and the conclusions suggested are interesting and sometimes surprising; they are, of course, to a considerable extent preliminary, but they indicate that much is to be learned by continued study along the lines that Dr. Draper has been following.



THE EDUCATION OF MEXICAN AND SPANISH-SPEAKING CHILDREN IN TEXAS.

By Herschel T. Manuel
The Fund for Research in the Social Sciences
\$1.25 net 6 x 9; ix + 173 Austin, Texas

The author considers this report little more than a preliminary survey. His contribution, however, is of value in opening up the field and pointing the way for future work. Some of the salient points which he brings out are as follows:

About 13 per cent of the total scholastic population in Texas is Mexican. Mexican children come from homes representing all degrees of economic and social status from the highest to the lowest. The prevailing picture, however, is one of under privilege—often extreme. Among the factors responsible for the generally unfavorable standing of the Mexican children in Texas schools are the following: (a) lack of knowledge of the English language; (b) the low social-economic status and cultural level of a large proportion of the population; (c) inferior school opportunities; (d) unsuitability of measuring instruments to reveal clearly the extent and nature of differences in racial groups. Nearly half of the Mexican children who are in school at all are in the first grade, nearly $\frac{3}{4}$ in the first three grades and only 3 or 4 per cent in the high school. In colleges and universities of Texas, the number of Mexicans is less than $\frac{1}{4}$ of 1 per cent of their scholastic population.

The author found that in some localities there was wide spread discrimination against Mexican children in the provision made for their public education. No doubt one of the reasons for this is the hygienic conditions among the children of the lowest social level. The report includes a large number of statistical tables, distribution maps and a bibliography. There is no index.

THE PSYCHOLOGY OF ACHIEVEMENT.

By *Walter B. Pitkin* Simon and Schuster
\$3.50 $5\frac{1}{4} \times 7\frac{3}{4}$; xi + 502 New York

We are a little disappointed to find a stylistically clever but nevertheless superficial piece of writing coming from an author, some of whose works we had heretofore rather admired. But the book does contain some gorgeous contributions to human biology.

Babe Ruth's eyes are the best of five pairs. His ears are the best of five pairs. So his combination of eyes and ears is the best out of twenty-five men. His general attention is the best out of one hundred men. So the combination of his eyes, ears, and general attention is the best out of 2,500 citizens. His nervous ability is the best out of 500 men. So the combination of this with the three preceding sets of traits, make him the best out of $2,500 \times 500$, or 1,250,000 people. And we still have to reckon with his amazingly high resistance to fatigue and his muscular strength.

Underneath all of these we find, as the solid foundation of his physical genius, an amazing basal metabolism. The Babe, for many years, has eaten about ten meals a day. And his radiant heat is so intense that he cannot wear even the lightest underwear on the coldest day of winter.

Had we the figures here on all these characteristics, we should find that Babe Ruth, far from being a 'man in a million,' is at least one man in fifty or sixty million.

For the layman this book probably has much more practical value than the "Sweet babble of the success cult." The

author develops from a new angle the good old maxim "If at first you don't succeed, try, try again."

SOME BIOLOGICAL ASPECTS OF WAR.

By *Harrison R. Hunt* Galton Publishing Co.
\$2.00 6 x 9; 118 New York

An attempt to investigate some of the effects of war on the genetic constitution of the population of the United States. The bulk of the study consists of a comparison of enlistment and death rates of Harvard College graduates, with similar rates for the country as a whole. It is shown that both enlistment and mortality rates were higher for the Harvard graduates, a result which the author regards as biologically unfortunate. The value of the study is reduced by a lack of clarity in exposition.

ERGEBNISSE DER SPORTÄRZTLICHEN UNTERSUCHUNGEN BEI DEN IX. OLYMPISCHEN SPIELEN IN AMSTERDAM 1928.

Papers by *A. Bethe and E. Fischer; C. Bramwell and R. Ellis; M. and H. Bürger and P. F. Petersen; F. Deutsch; J. Dybowska and W. Dybowski; A. Fessard and H. Laugier; F. Heiss; H. Herxheimer; S. Hoogerwerf; O. Huntemüller; W. Koblrausch; R. E. Mark; P. Schenk and K. Craemer; J. Snapper and A. Grünbaum; W. Thörner.* Edited by *F. J. J. Buytendijk.* Julius Springer

$6\frac{1}{2} \times 9\frac{1}{2}$; vii + 230 (paper)
12 marks Berlin

An interesting collection of papers, representing observations taken on participants in the Amsterdam Olympics. It is unfortunate that refusal to cooperate on the part of the officials of some of the larger nations (in particular the United States and England) reduces very considerably the number of noteworthy performers. For example, in Bramwell and Ellis' paper

on clinical observations, 202 athletes were examined; of these one man won the 100 and 200 metres; and the first and second place winners in the weight lifting were also examined. It is to be hoped that the officials in charge of the 1932 Olympics will assist in arranging further studies of this nature.



THE HISTORY OF THE AMERICAN PEOPLE.

By John H. Latané Allyn and Bacon
\$2.00 $5\frac{1}{2} \times 7\frac{7}{8}$; xviii + 827 New York

This book is more than a revision of the author's *History of the United States*. While the narratives of wars have been reduced to a mere outline of the more important campaigns, and political history has been simplified by the omission of many details, chapters have been added dealing with social, economic, industrial, and artistic development. As a native of a border state Dr. Latané is able to give a more unbiassed interpretation of the difficulties between the North and the South than many earlier text-book writers.



NOTES ON THE NATIVES OF CERTAIN VILLAGES OF THE MANDATED TERRITORY OF NEW GUINEA.

Visited During the Voyages of the Government Steam Yacht "Franklin," January-March, 1925. Anthropological Report No. 1.

NOTES ON THE NATIVES OF E MIRA AND ST. MATTHIAS. *Anthropological Report No. 2.*

CERTAIN NATIVES IN SOUTH NEW BRITAIN AND DAMPIER STRAITS. *Anthropological Report No. 3.*

By E. W. Pearson Chinnery
Commonwealth Offices, Australia House
Free London

$6 \times 9\frac{1}{2}$; Nos. 1 and 2 bound
together, 238 (paper)
No. 3, 102 (paper)

In these reports the Government An-

thropologist gives a fairly detailed account of the natives of the island of E Mira, together with miscellaneous notes on natives of the former German New Guinea, New Britain, and other adjacent islands. In most of the villages visited the number of children per marriage was small. The volumes constitute first rate contributions to the vital statistics of primitive races.



PRENATAL CARE. *United States Department of Labor. Children's Bureau Publication No. 4.*

U. S. Government Printing Office
10 cents Washington

$5\frac{3}{4} \times 9$; v + 71 (paper)

This excellent guide is not intended to make the expectant mother independent of the physician. Rather it has been prepared for those who are unable to consult a physician frequently and as a supplement to the doctor's instructions. Written briefly and simply, it contains the essential information which the pregnant woman should know. Included in the bulletin is a list of selected books of interest to mothers, a glossary and an index.



CHILDREN WHO RUN ON ALL FOURS And Other Animal-like Behaviors in the Human Child.

By Aleš Hrdlička
Whittlesey House (McGraw-Hill Book Co., Inc.)

\$5.00 6×9 ; xx + 418 New York

This book is a report on 387 infants who ran on hands and feet instead of creeping on hands and knees. The children in whom this and related animal-like behaviors occur are mostly strong and healthy both physically and mentally. Dr. Hrdlička concludes that "just as the human child before birth recapitulates, more or less, various phases of its physical ancestry, so the child after birth recapitu-

lates and uses for a time various phases of its prehuman ancestral behavior."

KONSTITUTIONSTYPEN DER KINDER

By W. S. Krasusky

S. Karger

4.20 marks

Berlin

7 x 10; vi + 62 (paper)

In the development of children there are periods in which they grow more rapidly in height, alternating with periods of lateral growth. With these cycles of physical development are associated changes in temperament. Can we discern, underlying these cycles, a constant substratum of habitus? Is the future pyknic distinguishable throughout his development from the future leptosome? Dr. Krasusky thinks not, although the complexity of the problem prevents any definite yes or no.

OUR CITY—NEW YORK. *A Book on City Government.*

By the High School Students of New York City.
Supervised by Frank A. Rexford

Allyn and Bacon

\$1.20 5 x 7½; xx + 344 New York

A book on city government prepared by high school students in the New York public schools under the guidance and advice of the teachers. It is a second edition, entirely rewritten, with new illustrations, and is designed for use by the pupils in their study of New York City, its government, finances, education, health regulations, etc. The illustrations are numerous. There is an index.

AN INTRODUCTION TO PHYSICAL ANTHROPOLOGY.

By E. P. Stibbe Longmans, Green and Co.

\$5.00 5½ x 8½; vii + 199 New York

A textbook for beginners, dealing with the technical knowledge necessary as a

foundation for work in physical anthropology. The subject is dealt with from three viewpoints: (1) Zoological, (2) Paleontological, and (3) Ethnological. Three chapters deal with practical applications, and exercises for the student. There is a glossary.

LEITFADEN DER ANTHROPOLOGIE

By K. Saller

Julius Springer

Berlin

24 marks (paper)

25.80 marks (cloth)

6¾ x 10; ii + 284

This excellent introduction to physical anthropology is written by a pupil of Martin. There are a brief bibliography and an index.

ZOOLOGY

A HISTORY OF APPLIED ENTOMOLOGY (*Somewhat Anecdotal*)

By L. O. Howard Smithsonian Institution
Washington

\$2.25

6½ x 9½; viii + 564 (paper)

The distinguished author of this delightful volume of somewhat rambling entomological reminiscences deserves well of his countrymen and of science generally. For it is a literal fact that he has done more than any other person who ever lived, first, to arouse public interest to a realization that insects are among the most formidable and menacing enemies to the continuance of human civilization, and, second, to devise and organize effective methods of defense against this menace. Doctor Howard has not only lived through the extraordinary rise of economic entomology to its present recognized importance among the agencies of human welfare. He has, to a remarkable degree, made it. Out of the wealth of contacts and intimate knowledge of persons and events which

his modest and self-effacing career as a public servant has somewhat automatically and necessarily entailed, he has accumulated a vast store of what current slang would call the "entomological dirt." Full of years and honors he has, quite apparently, had a lot of fun writing a book about it all. THE QUARTERLY REVIEW OF BIOLOGY ventures, in the name of all biologists, publicly to thank him for it.

The arrangement of the material is primarily geographical. Beginning with North America and going right around the world we are shown, in more or less detail according to circumstances, the history and present status of applied entomology in each country, with plenty of anecdotes along the way. Part VII deals with medical entomology, and with the use of predatory and parasitic insects as means of control. This latter field is one in which Doctor Howard has long been recognized as the outstanding leader. The volume ends with five half-tone plates of portraits of entomologists, and an index.

The book is a notable contribution to the history of biology.



DEMONS OF THE DUST. *A Study in Insect Behavior*

By William M. Wheeler

W. W. Norton and Co., Inc.

\$5.00 6 x 9; xviii + 378 New York

In this book Professor Wheeler deals with two groups of insects belonging to widely different orders but with remarkably convergent behavior. The neuropteran ant-lions and the dipteran worm-lions in their larval stage capture their prey by excavating funnels in the sand, at the bottom of which they lie in wait. The book treats the taxonomy, distribution, anatomy and life history of the two groups, much of the material being derived from the author's own researches. The

behavior of the larvae, he concludes, can not be analysed into simple or chain reflexes but must be considered "as a configuration, or 'Gestalt,' involving not only the insect but its specific environment as well." In conclusion he reviews the various predatory organisms that ambush instead of actively seeking their prey. These he dubs *lochêric*. Degeer's *Report on the worm-lion* and Réaumur's *History of the worm-lion fly* are given as appendices. There are also a bibliography of 26 pages and an index.

In his preface Professor Wheeler confesses his doubt whether he has not "crashed between two stools in attempting to interest both the entomologist and the general reader." No doubt the latter will skip much of the taxonomic and anatomic sections, but he will have only his own faint heart to blame if he allows these to scare him off from the fascinating historical and behavioristic sections. Altogether this is a great book, well worthy of its author.



THOMAS SAY. *Early American Naturalist.*

By Harry B. Weiss and Grace M. Ziegler

Charles C. Thomas

\$5.00 postpaid

Springfield, Ill.

6 x 9½; xiv + 260

This is a meticulously thorough and scholarly account of the life of an important figure in the history of biology in America. In fact Dr. L. O. Howard, in his Foreword says that Thomas Say ranks "as the most eminent of the early American taxonomic zoologists." Born in Philadelphia of Quaker stock Say started out to keep a drug store, but his love of natural history and his indifference to wealth combined to lead him quickly into the career of professional naturalist, from which he never deviated. His solid fame

rests most securely upon his entomological work.

The authors deserve great praise, not only for the thoroughness of the research which has gone into their work, but for the breadth of viewpoint with which the work was planned. We are given a comprehensive picture of Say's life *in its setting*, something unfortunately lacking in many biographies of scientific men.



RECENT ADVANCES IN ENTOMOLOGY.

By A. D. Imms

P. Blakiston's Son and Co., Inc.

\$3.50 net

Philadelphia

5½ x 8; viii + 374

This book "attempts to review and discuss certain aspects of the subject along which recent advances have been fertile in new facts and ideas." Chapter headings are as follows: Some aspects of morphology (two chapters); Metamorphosis; Palaeontology; The sense organs and reflex behaviour (two chapters); The fundamental aspect of coloration; Some aspects of ecology (two chapters); The practical application of ecology (two chapters); Parasitism (two chapters); Biological control (two chapters).

The book contains illustrations, tables, and diagrams. Literature lists are frequently appended to the chapters and there are author and general indices. Advanced students of entomology and investigators in general biological problems will find this book of much interest.



LA PARTHÉNOGÈSE.

By A. Vandel

G. Doin et Cie

32 francs 4½ x 6½; xix + 412

Paris

(paper)

A useful treatise on parthenogenesis, primarily concerned with its natural occurrence among animals. The successive

chapters cover: Discovery and interpretation, definition and extent, facultative parthenogenesis, cyclic parthenogenesis, paedogenesis, accidental parthenogenesis, parthenogenesis in nematodes, geographic parthenogenesis, the cytology of natural parthenogenesis, parthenogenesis in plants, the relations of experimental parthenogenesis to natural, parthenogenesis and sex, and general conclusions. The bibliography covers over seven hundred titles; there is both an author and a subject index.



HANDBOOK OF PROTOZOOLOGY

By Richard R. Kudo

Charles C. Thomas

\$5.50

Springfield, Ill.

5½ x 8½; x + 451

This is a handbook of interesting information on the common and representative genera of all the groups of both free-living and parasitic Protozoa. The text is in two parts. Part I consists of three chapters on morphology, physiology and reproduction of Protozoa. In the second part are thirty chapters dealing with the taxonomy, biology and development of common Protozoa. The author has gathered together much material which until now has been widely scattered and unavailable to the average student. The work includes keys, numerous excellent illustrations, reference lists for each chapter, and a detailed index.

A useful handbook for teachers, field workers, physicians, veterinarians and public health workers.



THE FUR SEAL OF THE CALIFORNIA ISLANDS *with New Descriptive and Historical Matter.* Zoologica, Volume IX. Number 12.

By Charles H. Townsend

New York Zoological Society

Zoological Park, New York City

6¼ x 9¼; 15 (paper)

This paper is an account of a species that was long supposed to be extinct. Weather-worn skulls found on Guadalupe Island, Lower California, in 1892 by the author showed it to be an undescribed species. It was named *Arctocephalus townsendi* by Merriam.

The species reappeared at Guadalupe in 1928 and two adult males were sent to the Zoological Garden at San Diego where they were photographed. When they died a skin and skeleton were presented to Dr. Townsend, who here describes skin and perfect skull from the first animal available for the purpose.

The paper contains new matter relative to its slaughter in the nineteenth century. It is illustrated with a colored plate and several photographs.

DIE TIERWELT DER NORD- UND OSTSEE. *Lieferung XVIII.*

Edited by G. Grimpe and E. Wagler

Akademische Verlagsgesellschaft m.b.H.

13.50 marks

Leipzig

6 x 8½; 147 (paper)

DIE TIERWELT DER NORD- UND OSTSEE. *Lieferung XIX.*

Edited by G. Grimpe and E. Wagler

Akademische Verlagsgesellschaft m.b.H.

12.80 marks

Leipzig

6 x 8½; 136 (paper)

These two parts of this useful survey of the fauna of the North and Baltic seas, previous numbers of which have been noted in these columns, deal with the following groups: Phyllopoda, by W. Rammner; Isopoda genuina, and Anisopoda, by H. F. Nierstrasz and J. H. Schuurmans Stekhoven, Jr.; parasitic Peridinea, by E. Reichenow; Kamptozoa, by C. I. Cori; and thalassobiontic and thalassophile Diptera Brachycera, by O. Karl.

HANDBUCH DER BIOLOGISCHEN ARBEITSMETHODEN. *Lieferung 346.*

Containing following articles: *Materialbeschaffung, Lebendbeobachtung und Haltung von Tardigraden*, by Ernst Marcus; *Sammeln, Züchtung und Untersuchung von Zecken*, and *Sammeln, Züchtung und Untersuchung der Flöhe*, by E. N. Pawlowsky; *Methodik der Erforschung der subterranean Fauna*, by P. A. Chappuis.

Urban und Schwarzenberg

13 marks 7 x 10; 226 (paper) *Berlin*

In this number of the *Abderhalden Handbuch* the most interesting articles to the general biologist are those on the tardigrades and the subterranean fauna; those on the culture of ticks and fleas will be useful to the parasitologist.

ENTWICKLUNGSPHYSIOLOGIE DER TIERE. *Wissenschaftliche Forschungsberichte Band XXII.*

By Paul Weiss

Theodor Steinkopff

11 marks (paper)

Dresden and Leipzig

12.20 marks (bound)

6 x 8½; xi + 138

This excellent little book presents the physiology of development with special reference to the advances of the last dozen years.

THE FAUNA OF BRITISH INDIA, INCLUDING CEYLON AND BURMA. *Cestoda. Vol. II*

By T. Southwell

Taylor and Francis

15 shillings 6 x 9; ix + 262

London

The second volume of this monograph is devoted to the Tænioidea. It also contains classified lists of Indian cestodes and their hosts and an index.

THE WATER EXCHANGES OF LIVING CELLS. I. *The Normal Permeability of the Eggs of Some Marine Invertebrates. University of California Publications in Zoology, Vol. 36, No. 7.*

By James L. Leitch

University of California Press

25 cents 7½ x 10½; 14 (paper) *Berkeley*

NOTES ON THE GENUS ENDO-
SPHAERA ENGELMANN AND ON ITS
OCCASIONAL HOST OPISTHONECTA
HENNEGUYI FAURÉ-FREMIET. *Uni-
versity of California Publications in Zoology*,
Vol. 36, No. 5

By James E. Lynch and Alden E. Noble.

University of California Press

25 cents $7\frac{1}{8} \times 10\frac{3}{4}$; 18 (paper) Berkeley



A STUDY OF THE SPECIES OF EIM-
ERIA OCCURRING IN SWINE. *Uni-
versity of California Publications in Zoology*,
Vol. 36, No. 6.

By Dora P. Henry

University of California Press

25 cents $7\frac{1}{8} \times 10\frac{3}{4}$; 12 (paper) Berkeley



THE MORPHOLOGY AND LIFE-
CYCLE OF OXYMONAS DIMORPHA
SP. NOV., FROM NEOTERMES SIMPLI-
CICORNIS (BANKS). *University of Cali-
fornia Publications in Zoology, Volume 36*,
No. 2.

By Frank H. Connell

25 cents $7 \times 10\frac{3}{4}$; 16 + 3 plates (paper)



HYPERMASTIGOTE FLAGELLATES
FROM THE TERMITE RETICULI-
TERMES: TORQUENYMPHA OCTO-
PLUS GEN. NOV., SP. NOV., AND TWO
NEW SPECIES OF MICROJOENIA.
*University of California Publications in
Zoology, Volume 36, No. 3.*

By Virginus E. Brown

University of California Press

25 cents $7 \times 10\frac{3}{4}$; 12 + 5 plates (paper) Berkeley



COPEIA. *A Journal of Cold-Blooded Verte-
brates. Established in 1913. The David
Starr Jordan Anniversary Number. 1930*,
No. 4.

*American Society of Ichthyologists
and Herpetologists*

50 cents

Ann Arbor, Michigan

Subscription price of journal (quarterly)
\$2.00 per annum

$6\frac{3}{4} \times 9\frac{3}{4}$; 76



BOTANY

SIZE AND FORM IN PLANTS. *With
Special Reference to the Primary Conducting
Tracts*

By F. O. Bower

The Macmillan Co.

\$4.50 $5\frac{3}{4} \times 8\frac{1}{2}$; xiv + 232 New York

No better conception of this important
book can be given than by quoting certain
passages from the author's preface. He
says

"In approaching a problem so extended as that of
the relation between Size and Form in Plants at
large, it is desirable in the first instance to select some
limited field of observation: preferably it should be
one in which those difficulties, which increasing size
necessarily entails, have not been so successfully sur-
mounted by adaptation as they have been in some of
the Highest Plants. The features compared should
also be readily open to measurement, whether the
material be in the living or in the fossil state. The
conducting tracts, and in particular the wood which
is as a rule well preserved in fossils, afford the best
opportunity for comparative treatment." "Under
the name 'Size-Factor' is connoted that influence
which tends to secure by modification of Form a due
levelling up of the proportion of surface to bulk as
the Size increases. Whatever that influence may be,
the measurements of growing plants that depend on
primary development show consistently its effect in
modifying Form, external or internal. It may be
described as a Morphoplastic Factor. The evidence
that it does act in moulding the tissues is widespread,
and its incidence is insistent and unavoidable. The
development of this conception and a detailed record
of the results of its action form the substance of this
book." His aim has been to follow a middle course
between the physiologists who study function, and
the morphologists who study form. "... certain
structural facts have been stated in their relation to
function: in fact they have been treated organogra-
phically. For this purpose a very considerable field
of observation has been advanced, with approximate

rather than absolute measurements. Certain conclusions as to Size and Form have followed, and they are set down here in their biological aspect. It is the hope of the author that by venturing thus upon a comprehensive statement of fact and inference from the side of Morphology, the problems of the physiologist may present themselves with an added interest and point, and that the result may be a better common understanding.

The text of the book is devoted to a study of the Pteridophyta, both living and fossil forms. There are also sections on the shoots of seed plants, and on roots and a chapter on the plasticity of form and structure in relation to size. The work includes tables of measurements and ratios, 72 figures, mostly cross sections of stems and roots, and an index.

ELEMENTS OF PLANT SCIENCE

By Charles J. Chamberlain

McGraw-Hill Book Co., Inc.

\$1.90 5 $\frac{3}{8}$ x 8; xii + 394 New York

This excellent introduction to the study of plants will be extremely useful in schools giving a beginning course in botany. It is so arranged that it can be used in places where microscopes are not available and only one semester is given to plant study. It provides, however, for a year's work and covers, in outline, a considerable part of the subject matter of botany. The many carefully selected illustrations and the section on laboratory methods add greatly to the value of the book. There is an index.

RUBBER. *An Economic and Statistical Study.*

By José Carlos deM. Soares

Richard R. Smith, Inc.

\$3.00 5 $\frac{1}{2}$ x 9; xii + 93 New York

An exhaustive survey of the history of the decline of the rubber industry in Brazil, the causes of the decline, and the growth of competition in foreign countries. The author also incorporates in the book plans for the future reorganization of the indus-

try which should lead to the rehabilitation of one of Brazil's chief sources of wealth. Much statistical material is given on world production and consumption of rubber, profits and dividends of rubber companies, duties on rubber, etc. There is no index.

PLANT ECOLOGY. *Second Edition, Thoroughly Revised*

By W. B. McDougall

Lea and Febiger

\$3.00 net

5 $\frac{1}{4}$ x 7 $\frac{3}{4}$; 338 Philadelphia

OBSERVATIONS SUR LA BIOLOGIE DE QUELQUES CHAMPIGNONS.

By Roger Martin

40 francs net

6 $\frac{1}{2}$ x 10; 115 (paper)

ÉTUDE COMPARATIVE DE BACILLUS MESENTERICUS FUSCUS FLÜGGE ET DE BACILLUS MESENTERICUS NIGER LUNT. *Thèse présentée et soutenue publiquement le Mercredi 2 Juillet 1930 à la Faculté de Pharmacie de Nancy pour obtenir le titre de Docteur de l'Université de Nancy (Mention Pharmacie)*

By Pierre Thomas

40 francs net

6 $\frac{1}{2}$ x 10; 138 (paper)

TRAVAUX DU LABORATOIRE DE MICROBIOLOGIE DE LA FACULTÉ DE PHARMACIE DE NANCY.

By MM. Lasseur and Vernier

6 $\frac{1}{2}$ x 10; 189 + 7 plates

CONTRIBUTION A L'ÉTUDE DE LA COLORATION DE GRAM. *Étude Critique de la Coloration de Gram. Essai sur la Modification de Gottstein. Essai de Stabilisation de la Solution Colorante de Violet de Gentiane Phéniqué.*

By Georges Coudray

40 francs net

6 $\frac{1}{2}$ x 10; xii + 112 (paper)

CONTRIBUTION A L'ÉTUDE DE LA PRÉCIPITATION ET DE L'AGGLUTINATION SÉRIQUES DES CHAMPIGNONS.

By Paul Martin

60 francs net

6½ x 10; 211 + 5 plates (paper)

CONFÉRENCES FAITES AU LABORATOIRE DE MICROBIOLOGIE DE LA FACULTÉ DE PHARMACIE DE NANCY.

By G. Darmon, M. Dufour, A. Travers, G. Vavon, Pierret, R. Collin, Ph. Guinier, Ed. Gain, L. Nègre, Patriat and P. Vitu.

Laboratoire de Microbiologie de la Faculté de Pharmacie de Nancy

Nancy

60 francs net

6½ x 10; 271 (paper)

LES VARIATIONS LAURENTIENNES DU POPULUS TREMULOIDES ET DU P. GRANDIDENTATA. *Contributions du Laboratoire de Botanique de l'Université de Montréal.*—No. 16.

By Frère Marie-Victorin

50 cents 6 x 9; 16 (paper)

LE GENRE RORIPPA DANS LE QUÉBEC. *Contributions du Laboratoire de Botanique de l'Université de Montréal.*—No. 17.

By Frère Marie-Victorin

Laboratoire de Botanique Université de

Montréal

Montreal

50 cents

6 x 9; 17 (paper)

L'ANACHARIS CANADENSIS. *Histoire et solution d'un imbroglio taxonomique. Contributions du Laboratoire de Botanique de l'Université de Montréal.* No. 18.

By Frère Marie-Victorin

Université de Montréal

Montreal, Can.

75 cents

6 x 9; 43 (paper)

REPORT ON THE PREPARATION OF FRUIT FOR MARKET, (*Part II: Gooseberries, Currants, Cherries, Raspberries, Loganberries, Tomatoes, Cucumbers and Grapes*).

Economic Series No. 24.

Ministry of Agriculture and Fisheries

H. M. Stationery Office

London

British Library of Information

551 Fifth Ave., New York

6 d. net 6 x 9½; 98 (paper)

MORPHOLOGY

THE ORIGIN OF THE HUMAN SKELETON. *An Introduction to Human Osteology*

By R. Broom

H. F. and G. Witherby

10s. 6d. net 5½ x 8¾; 164

London

For thirty odd years Dr. Broom has been studying fossil forms of South African mammal-like reptiles in an endeavor to find the ancestor of the mammals. His investigations have led him to believe that he has been successful in tracing the origin of mammals and in solving the problem of the origin of lizards and crocodiles. Important facts have also appeared bearing on the evolution of the dinosaurs and birds. Pending the completion of a monograph on his researches he has issued this book which, in briefer form, presents the main results of palaeontology bearing upon the structure of the mammals. While designed for the student of anatomy, teachers of biology will find it full of interesting material for the general student. It is a comparative anatomy of the vertebrate skeleton from the fishes to the amphibians and primitive reptiles, the mammal-like reptiles and the mammals. The work includes many well chosen illustrations, a diagram of the evolution of the different forms, a bibliography and an index.

PRINCIPLES OF FUNCTIONAL ANATOMY OF THE RABBIT

By Edward D. Crabb

P. Blakiston's Son and Co., Inc.

\$1.50 5½ x 8¼; ix + 137 Philadelphia

Teachers of general biology and pre-medical students, and of students majoring in physical education, will find this an excellent guide for a course in elementary anatomy. Emphasis is put on the functional rather than on the purely descriptive point of view. The entire outline may be covered in something like one hundred hours of laboratory work. In two preliminary sections the author describes (a) the necessary laboratory equipment and material and (b) the elementary tissues. The book is sufficiently illustrated and contains an index.



L'ŒUF et les Facteurs de l'Ontogénèse.

By A. Brachet

Gaston Doin et Cie

32 francs 4½ x 7; 438 (paper) Paris

In this second edition of Professor Brachet's book on causal embryology, a subject which owes so much to his researches, the chapters on maturation, the inertia of the unfertilized egg, fecundation, and parthenogenesis have been rewritten, and a new chapter on organizing centers and germinal localizations has been added.



PHYSIOLOGY AND PATHOLOGY

LES PHÉNOMÈNES DE CHOC DANS L'URTICAIRE. (*Étude Clinique et Thérapeutique*).

By Pasteur Vallery-Radot and Lucien Rouquès.

Masson et Cie

35 francs 6 x 9¼; 232 (paper) Paris

Anyone who has ever treated many patients with urticaria will welcome information on the subject. Everyone assumes that urticaria is due to eating some food to which the body is sensitive; the trouble

is to find the food. Sometimes the hives continue to appear even when the patient is desperate enough to go for a week without eating. Actually, it is now coming to be recognized that there are other causes for urticaria such as nervous shock, muscular effort, and exposures to heat and cold. Some persons get urticaria when they lose their temper.

In this book the authors prefer to use the term "Colloidoclastic crisis," instead of the old term "hemoclastic crisis," because the phenomenon concerned is not limited to changes in the blood. There are at least four types of urticaria; the first is due perhaps to a fairly simple anaphylaxis. The second is due to reactions more complicated than those of simple anaphylaxis as the changes in the body are brought about slowly and insidiously and as a result of repeated contacts with antigen. In the third group the first contact of the patient with the antigen seems to be enough to produce the reaction, and one must assume that the subject possesses from the start an idiosyncrasy, probably hereditary in nature. In the fourth group the urticaria is produced without the intervention of any antigen coming from outside the body.

The book is interesting and readable. Many points are illustrated with brief case histories; but some readers will doubtless disagree with the interpretations made. The various methods of treatment now being used in France are described and conservatively appraised. There are a number of interesting charts showing the ways in which the leucocyte count changes from hour to hour during an attack of urticaria.



LE SYSTÈME GLANDULAIRE ET VUES NOUVELLES EN MÉDECINE.

By Francesco Cavazzi

Gaston Doin et Cie

14 francs 7 x 10; 45 (paper) Paris

ON PEUT RAJEUNIR. *La fonction énergétique de la sécrétion interne testiculaire et les injections sous-cutanées de produits de sécrétion interne testiculaire pour redonner les énergies organiques aux hommes affaiblis par l'âge et par le travail et pour prolonger leur vie. Rapport de faits expérimentaux.*

By Francesco Cavazzi Gaston Doin et Cie
25 francs Paris

7 x 10; 68 + 21 portraits (paper)

These two treatises go together. The first is supposed to furnish the rational foundation for the second, which sets forth the alleged consequences of the supposedly practical application of what the author believes to be physiological principles, with that naïve optimism which is such a delightful characteristic of the Latin races when their digestions are working well. The general idea is that if one injects subcutaneously into old and enfeebled men "*de produits de sécrétion interne testiculaire*," the old boys become once more parabolic, hydraulically speaking, and in other ways which Reginald, the Office Boy, says we musn't mention in a family magazine, get back on the up and up pathway. The second volume shows serial photographs of some of the patients, taken before, during, and after. In their stern and purposeful lugubriosity they are reminiscent of the Smith Bros., Trade and Mark. The trouble about it all is, first, that we are nowhere told precisely what it is that is injected, how it is obtained, or what the dosage is; and, second, that the evidence of rejuvenation which is presented would not convince even a beginning biology student in Bryan University, Dayton, Tennessee.

HYPERTENSION

By Leslie T. Gager

The Williams and Wilkins Co.

\$3.00 6 x 9; xiii + 158 Baltimore

This review of the literature of hyperten-

sion will be found very useful as a reference work. Its point of view is primarily clinical. Furthermore the author is soundly conservative. The truth is, and it is an odd fact considering the enormous amount of effort which has been put upon its study, that while a great deal is known about hypertension as a phenomenon, extremely little is known of its essence, its causation. In the meantime, as Doctor Gager says (p. 88): "The future of patients with arterial hypertension, as a group, falls within limits so definite in respect of longevity and mode of death as to have almost the force of natural law. The prognostic significance of high blood pressure has been firmly established by the data of life insurance medicine."

There is a bibliography of 505 titles and detailed author and subject indexes.



THE CLINICAL INTERPRETATION OF BLOOD EXAMINATIONS

By Robert A. Kilduffe Lea and Febiger

\$6.50 net 5 3/4 x 9 1/4; 629 Philadelphia

This extensive survey of blood tests and their clinical indications, applications and significance will be of value to physicians. The author has incorporated in his book two treatises which he issued some years ago on (1) *The clinical interpretation of the Wasserman reaction* and (2) *The clinical interpretation of blood chemistry*. Both of these have been greatly amplified, revised and extended to cover the field of laboratory examinations pertaining to the blood. The important work of other investigators has been reviewed and the results presented for the benefit of those who are unable to go to the original sources. Not only those methods have been included whose value is definitely understood but also those methods whose value was presumable, though very questionable and in some cases even definitely disproved. The work includes

numerous figures and tables, literature references and a detailed index.



LA THÉRAPEUTIQUE MODERNE

By *Gabriel Florence* *Armand Colin*
10 francs 50 $4\frac{3}{4} \times 6\frac{3}{4}$; 202 (paper) *Paris*

This excellent little book is not a treatise on therapeutics, but an explanation for the general reader of some of its fundamental principles. In the first part are treated the biological problems of the intracellular penetration of therapeutic substances and their transformation by the organism. In the second part examples of the synthesis of new therapeutic agents by the chemist are given. The third part deals with immunity and anaphylaxis; the fourth, with vitamins and hormones. A résumé of the resolutions of the international conferences for the biological standardization of drugs and a bibliography conclude the book. There is no index.



HYPERSENSIBILITÉS SPÉCIFIQUES DANS LES AFFECTIONS CUTANÉES.

Anaphylaxie. Idiosyncrasie.

By *Pasteur Vallery-Radot et Mlle. V. Heimann* *Masson et Cie*

25 francs $6 \times 9\frac{3}{8}$; 146 (paper) *Paris*

This little book gives a clear exposition of the French views on the subject of cutaneous hypersensitiveness. The authors discuss different types of urticaria, edema and eczema, and describe the various methods used in attempting desensitization. They take up in detail also the various methods of diagnosis. The style is lucid and the book is readable. Many of the points made are illustrated by case histories. There are good indexes, and the bibliography is adequate, although there is a preponderance of references to

French writers. It is a worth while addition to books on this subject.



RIDERS OF THE PLAGUES. *The Story of the Conquest of Disease.*

By *James A. Tobey* *Charles Scribner's Sons*
\$3.50 $5\frac{3}{4} \times 8\frac{1}{2}$; xv + 348 *New York*

De Kruif's *Microbe Hunters* naturally comes to mind when reading this book. It is a pity, perhaps, for de Kruif's book was an exception to all rules. The present volume is entertaining popular scientific history; de Kruif's came close to genius. Tobey covers much more ground; and he is particularly interested in public health work. His book will furnish good entertainment for an evening's reading.



CHRONIC ARTHRITIS AND RHEUMATOID AFFECTIONS *with Recovery Record* By *Bernard L. Wyatt, with the Collaboration of Louis I. Dublin.*

William Wood and Co.

\$2.50 $5\frac{1}{2} \times 8\frac{1}{2}$; ix + 166 *New York*

Although arthritis and the rheumatic affections rank low as causes of death, they are responsible for a vast amount of suffering and economic loss. This book on their treatment emphasizes the importance of early diagnosis and the fact that many of the sufferers can be greatly improved in condition or even cured.



LE CHOC ANAPHYLACTIQUE ET LE PRINCIPE DE LA DÉSENSIBILISATION

By *A. Besredka* *Masson et Cie*

30 francs $5\frac{1}{2} \times 9$; 276 (paper) *Paris*

In this monograph Professor Besredka tells what is known of the curious phenomenon of anaphylaxis. Of especial interest is his account of his experiments on antianaphylactic vaccination.

MÉTABOLISME ET FONCTIONS DES CELLULES. *Esquisse d'une Physiologie des Réactions Productrices d'Énergie dans la Cellule Vivante.*

By L. Genevois
26 francs

Masson et Cie
Paris

6½ x 9½; vii + 118 (paper)

This is a review, for French readers, of the researches on cell metabolism of Meyerhof and Warburg and their students and followers. It is very well done. There is an extensive bibliography, but no index.

ANNALS OF THE PICKETT-THOMSON RESEARCH LABORATORY. Vol. VI. *The Pathogenic Streptococci. The Role of the Streptococci in Scarlet Fever.*

The Williams and Wilkins Co.
\$10.00 Baltimore

8½ x 11; xiii + 470 (paper)

Bailliere, Tindall and Cox
£2, 2s. net London

BIOCHEMISTRY

LE PH ET SA MESURE

By M. Huybrechts
15 francs 4¼ x 7½; 227 (paper) Paris

This clearly written little book will be useful to those who want to know what hydrogen ion concentration means, and how it is measured, but who lack the knowledge of physical chemistry necessary to understand the more technical treatises on the subject.

DONNÉES NUMÉRIQUES DE BIOLOGIE.

BIOLOGY (Numerical Data). *Extracted from Volume VII of Annual Tables of Constants and Numerical Data (years 1925-1926).*

By E. F. Terroine and M.-M. Janot
Gauthier-Villars et Cie

60 francs (cloth)

55 francs (paper) Paris

8½ x 10½; xx + 68

An extract from Vol. VII of the Annual Tables published under the auspices of the International Research Council and of the Union of Pure and Applied Chemistry, covering the literature of 1925-26. The data are chiefly biochemical.

HANDBUCH DER BIOLOGISCHEN ARBEITSMETHODEN. *Lieferung 342. Con-*

ÜBER DAS PROBLEM DER BÖSARTIGEN GESCHWÜLSTE. *Eine experimentelle und theoretische Untersuchung. Zweiter, Abschliessender Band.*

By Lothar Heidenhain
42 marks (paper)
47.60 marks (bound)

Julius Springer
Berlin

10 x 13; vi + 207

The first volume of this admirable study of cancer was reviewed in the QUARTERLY REVIEW OF BIOLOGY for March, 1929. Further work confirms the author in his conclusion that the causative agent of cancer is a virus. The difference between the percentage of malignant tumors in inoculated mice and in controls is statistically significant.

DAS GEHEN. *Und seine Veraenderung durch verschiedene Umstaende. Auf Grund experimenteller Untersuchungen.*

By Adolf Basler

Verlag der Sun Yatsen-Universitaet
Canton

(European agent: Gustav Fock.

18 marks 7 x 10½; xi + 272 Leipzig)

A careful study of the kinematics and dynamics of walking, based in large part on the author's own experiments. There is an index.

taining following articles: *Potentiometrische Mikrotitration*, by Günther Rienäcker; *Pufferung und Puffersysteme*, by Franz Leuthardt; *Registrierung der Wasserstoffionenkonzentration im strömenden Blut*, by Robert Brinkman; *Die Bestimmung von Gas- und Dampfdrucken*, by Hans Fischer and Otto Rebmann.

Urban und Schwarzenberg
17 marks 7 x 10; 288 (paper) Berlin

This number of the Abderhalden *Handbuch* will be chiefly of interest to the biochemists and physiologists.



MIKROCHEMISCHES PRAKTIKUM.

Eine Anleitung zur Ausführung der wichtigsten mikrochemischen Handgriffe, Reaktionen und Bestimmungen mit Ausnahme der quantitativen organischen Mikroanalyse. Zweite Auflage.

By Friedrich Emich. (Mit einem Abschnitt über Tüpfelanalyse by Fritz Feigl.)

J. F. Bergmann
12.80 marks (paper) München
6 x 9 $\frac{1}{4}$; xii + 157 (paper)

A revised edition of a useful microchemical *vade mecum*.



PROXIMATE COMPOSITION OF FRESH VEGETABLES. U. S. Department of Agriculture Circular No. 146.

By Charlotte Chatfield and Georgian Adams
U. S. Government Printing Office
5 cents 5 $\frac{3}{4}$ x 9; 24 (paper) Washington



SEX

SEX GLANDS FUNCTION AND THE HUMAN LIFE.

By C. Leventis C. Leventis
\$2.00 911 Kresge Bldg., Detroit
5 $\frac{1}{4}$ x 7 $\frac{1}{4}$; 132

This little book is well adapted to

reading aloud in the biologist's home. We offer a few extracts:

Giving to all new born babies as a standard food, the cow's milk, and not their mother's milk, we will impress the glands in their function of all babies in a similar way. As a result all human beings will be of the same type of character, without individuality. They may be strong in their physical construction, but, in my opinion, they will be low in their mental power.

Grafting the gonads of the civilized human organism on the organism of chimpanzees or gorillas would be a profoundly interesting experiment. To me it is fraught with encouraging possibilities of success. There is little doubt that it would result in improving these wild organisms.

This could be probably accomplished in the following way:

The offsprings of chosen pairs of male and female gorillas would be grafted with human gonads very early in their lives before the reproductive function of the ape's gonads starts. During their lives they would receive injections of human serum. By treating their offspring in the same way for a few generations it might be possible to obtain a species nearer to the human race, if not quite resembling it. At least, the new species would be endowed with more human qualities than the gorilla. The intelligence of these animals could be developed by training and thus produce an educated and civilized species of animal which probably would form a missing link between the human race and the higher apes.

By such a procedure it is not impossible to impress the reproductive function of the gonads of the animals by the absorption and assimilation of the implanted human gonads and by the injection of the human serum. This might be followed by a spontaneous mutation into the gonads of that inferior animal organism, and thus help nature in its tendency toward evolution. In this event there would be produced a more accomplished and farther evolutionized living being, with developed reproductive elements for the preservation of its species.

Modern women, being free to gratify their erotic feeling by exposition of their body, do that in a rather scandalous social manner to the great harm of their other feelings and charms. If they endeavor to excuse this by saying that they do so in order to be more attractive to men, they are mistaken. On the contrary, they spoil that prestige of the hidden and occult upon the men. Arms and legs of women are not comparable to the different bottles of liquor exposed in the windows of shops before prohibition.

We passed them indifferently. Now that such bottles are mysteriously hidden their attractiveness is greatly magnified.

Women must abandon and forget most of their feminine sex impetus for a more respectful social life, otherwise fathers, brothers, sons, and school boys will not avoid evil suggestions and thoughts through the impressions arising from seeing the naked legs of their daughters, teachers, sisters and mothers. We have many such examples today.



HEALTH AND CONTINUAL YOUTH.

By *Mary Marriott Radcliffe*.

The Norman Remington Co.

\$2.00 9 x 12; 19 *Baltimore*

This beautifully produced book maintains the odd thesis that the congress of the sexes is biologically harmful. In the actual words of the author

These pages give evidence of the injury of sex to health, morale and duration of life, and the logical and ideal solution, with supporting evidence, that mankind shall overcome disease and death, and keep alive the clean, gay, vibrante [*sic*] spirit of youth—through steadily increasing and total sex abstinence, sunlight, rest, diet and other necessary hygiene.

We are unable to discover in the book any evidence which, in our opinion, is either valid or pertinent so far as concerns that part of the thesis pertaining to the relation of "sex abstinence" to "disease and death."

There is included a long table of figures, furnished chiefly by veterinarians, which gives estimates and opinions as to the extreme ages at death which may be attained by stallions, mares, geldings, oxen, and bulls. In our opinion the data in this table are so far at variance with the canons of sound statistical procedure, particularly relative to random sampling, as not to be worthy of any serious consideration whatever.

MARRIAGE. *Past, Present and Future.* *An Outline of the History and Development of Human Sexual Relationships.*

By *Ralph de Pomerai*

Richard R. Smith, Inc.

\$4.00 net

New York

5 $\frac{3}{8}$ x 8 $\frac{1}{2}$; xvii + 370

A survey of the history, present conditions, and desirable reforms in that state which St. Paul described as better than burning. The author has produced a moderately interesting book, though we are not always convinced by his arguments. Why, however, does he describe the author of *Erewhon* as "Bishop" Butler?



EARLY THEORIES OF SEXUAL GENERATION.

By *F. J. Cole*

Oxford University Press

\$6.00 5 $\frac{1}{2}$ x 8 $\frac{3}{4}$; x + 230 *New York*

This book is primarily concerned with the history of the Preformation Doctrine. The author has, on the whole, succeeded admirably in telling a clear and interesting story of what might appear a dull tangle of scientific speculation and error. The book is a valuable contribution to the history of science.



PHYSICIANS' MANUAL OF BIRTH CONTROL.

By *Antoinette F. Konikow*

Buchholz Publishing Co.

\$4.00 6 x 9; xiii + 245 *New York*

A treatise for physicians on the technique of contraception, on the whole well done. There is a statistical section based on the author's clinical experience; it is, unfortunately, as inadequate as all others we have seen as evidence of the real effectiveness of the techniques involved.

BIOMETRY

NUMERICAL ANALYSIS.

By James B. Scarborough

The Johns Hopkins Press

\$5.50 $6\frac{1}{8} \times 9\frac{1}{2}$; xiv + 416 *Baltimore*

A useful treatise for anyone who has occasion to obtain numerical results from his mathematics. The treatment is considerably more detailed and elementary than that in Whittaker and Robinson. As a result, a number of topics treated in the latter are not found in the present volume. On the other hand, the beginning computer will probably find this a less difficult work to follow.



LEÇONS SUR LA THÉORIE MATHÉMATIQUE DE LA LUTTE POUR LA VIE.

By Vito Volterra

Gauthier-Villars et Cie

60 francs

Paris

$6\frac{1}{2} \times 10$; vi + 214 (paper)

It is hoped that a detailed review of this book will appear in an early number of THE QUARTERLY REVIEW OF BIOLOGY.



PSYCHOLOGY AND BEHAVIOR

ANIMAL DRIVE AND THE LEARNING PROCESS. *An Essay Toward Radical Empiricism. Vol. I. (With a supplementary essay on "This Material World," by Harold C. Brown).*

By Edwin B. Holt

Henry Holt and Co.

\$2.50 $5\frac{1}{4} \times 8$; x + 307 *New York*

This book is a presentation of psychology in purely physiological terms, based in large part on Bûk's principle of the reflex circle. The first volume deals with the development of the simpler types of behavior, while the second will treat the higher psychic functions. With

our present limited knowledge of neural physiology much of the account is necessarily hypothetical, but it is well worth while to show that psychological phenomena can be reasonably stated in terms of known types of physiological process, even though the proof or disproof of the details must be left to future experiment.

Dr. Holt has a pungent wit and is not afraid to speak out in meeting as is shown by the following and other passages:

The sexual appetite is so hedged about by taboos, superstitions, and lies, that any true statement about it will meet with a thousand frenzied denials. So if I say that the sexual appetite, like all other appetites, is imperative and like the others does not brook indefinite delay, there will be loud cries of dissent, to the general purport that "pure thoughts, hard exercise, cold water and prayer" will divert the sexual appetite for a lifetime. To those in whom the sexual appetite arouses "impure thoughts" I make no doubt that cold water and prayer will prove beneficial. For indeed I suppose that the most, and perhaps the only, impure thought connected with sex is the thought to perpetuate the stereotyped lies about it. But if there is anybody who honestly imagines that this appetite ever has been or ever will be beguiled by any such precautions, he should find his attention instantly claimed by the attractive themes of sexual perversion and the neurotic disorders, and *why they happen*. He will also find it interesting and profitable to study the phenomena of "cultural" mendacity, and the "as if" hypocrisies. And yet even the Freudians, who ought to know better, follow the accepted superstitions with their theory of sexual "sublimation"—a colossal blunder—and the unctuous rubbish about "cultural" (*kulturrelle*) aims. Of course, if by artificial, "educational" means this or any other appetitive restlessness is drafted off into motor channels other than those that appease the appetite, the individual is successfully wrecked.



CONDITIONS AND CONSEQUENCES OF HUMAN VARIABILITY.

By Raymond Dodge *Yale University Press*

\$2.50 6×9 ; xi + 162 *New Haven*

The older generation of physicists were

accustomed to look down their noses at biology and especially at psychology. The study, we were told, of systems in which differences in the internal relations might make wide changes in the results obtained from successive trials with the same experimental set-up could scarcely be dignified with the name of science. Present-day physicists, having learned something of the caprices of the electron, are less snooty. Professor Dodge, however, glories in this infirmity of psychology and finds

Variability to be not a mere accident impeding the development of a true science of behavior, experience, and personality, but rather an aspect of the observable facts that is quite as important as their commonly noticed relative stability. The conditions of variability reach into the elementary processes of neural action until one may say that a differential variability is the hypothesis that best fits the observable neuropsychological facts.

The consequences of variability seem to reach into the very heart of mental reaction and mental development. One may say with some confidence that without variability there would be no mental development, either in the race or in the individual. The evidence suggests an even more fundamental relationship. One is tempted to substitute for the older materialistic doctrine, "Without phosphorus no thought," a newer psychophysiological generalization, "Without variability, no mind." But the variations must apparently be of definite and distinctive kinds, connected in a specific manner with systematizations of relative persistency.

THE MIND OF THE MURDERER.

By Harold Dearden

Sears Publishing Co., Inc.

\$3.50 $5\frac{1}{2} \times 8\frac{1}{2}$; 288 New York

A tiresome piece of ostensibly "popular" scientific writing, of a sort calculated to make the judicious tearful. The technique is to take a murder case, as described in the newspapers or in earlier popular treatises on famous trials, and then try to concoct some sort of a psychological "explanation" of the mur-

derer's supposed motives. The actual legal evidence of record is frequently strained, and sometimes even thrown overboard, to help in the development of the theory to fit a particular crime. Twenty cases are picked out for this so-called "psychological" treatment, going back as far as 1800. Those with a cultivated taste for the literature of crime will not be amused by this book. As compared with Roughead's delightful books in that field this is very poor pap indeed. There is no index, but it doesn't matter.

THE RELATIONS OF PSYCHOLOGY TO MEDICINE AND THE RECOGNITION AND TREATMENT OF COMMONER AFFECTIVE DISORDERS. *Porter Lectures Series I.*

By Lewellys F. Barker

University Extension Division, University of Kansas

75¢ (paper)
\$1.00 (cloth)

Lawrence

$5\frac{3}{4} \times 8\frac{1}{2}$; 68

A series of three lectures delivered at the School of Medicine at the University of Kansas, under the Porter Foundation. The subjects of the lectures are as follows: (1) The Relations of Psychology to Medicine; (2) On Certain Disturbances of the Whole Personality with Especial Reference to the Commoner Affective-Conative Disorders; (3) Treatment of Personality Disorders, Especially of the Commoner Affective Disorders. The author, widely known for his eminence as a physician and teacher at the Johns Hopkins School of Medicine is well fitted to deal with these subjects. He emphasises the need of a knowledge of psychology and a thorough training in psychological methods of investigation for those engaged in medical work, the importance of being well acquainted with the criteria necessary for

the recognition of the disturbances of feeling emotions in the different psychoneuroses, and outlines a comprehensive plan of therapy.

Each section contains lengthy literature lists. There is no index.



THE GUIDANCE OF MENTAL GROWTH IN INFANT AND CHILD.

By Arnold Gesell *The Macmillan Co.*
\$2.25 $5\frac{1}{2} \times 8\frac{1}{2}$; xi + 322 New York

The author is Director of the Yale Psycho-clinic and Professor of Child Hygiene in Yale University. The present volume is made up of a somewhat varied collection of papers dealing with different phases of mental growth and child training. The most interesting chapter, to us, was that on the training given her children by John Wesley's mother. For instance, her children were taught to read at the age of five: "One day was allowed the child wherein to learn its letters; and each of them did in that time know all its letters, great and small, except Molly and Nancy who were a day and a half before they knew them perfectly."



RACE PSYCHOLOGY. *A Study of Racial Mental Differences.*

By Thomas R. Garth
Whittlesey House (McGraw-Hill Book Co., Inc.)

\$2.50 $5\frac{1}{2} \times 8$; xiv + 260 New York

A review of what is actually known about the comparative psychology of man. The author thinks that the evidence at present available is inadequate to establish the existence of real racial differences; even in the case of the intelligence tests, where the evidence is reasonably satisfactory that the actual I.Q.'s of, e.g., the

negro are lower than that of the whites, it is suggested that an unknown but possibly large part of the difference may be due to cultural and social factors, rather than to racial differences.



THE SIGNIFICANCE OF DELAYED REACTIONS IN YOUNG CHILDREN. *Comparative Psychology Monographs, Vol. 7, No. 4, Serial No. 34.*

By Magda Skalet *Johns Hopkins Press*
\$1.50 $6\frac{3}{4} \times 10$; 82 (paper) Baltimore

A study of the responses after a longer or shorter interval to such situations as the placing of a cookie under one of three dishes or the showing of one of a set of geometric forms. Some children, it was found, could remember the plate under which the cookie had been put for as long as 34 days. To anyone acquainted with children, this is an entirely credible result.



CHILD PSYCHOLOGY.

By Margaret W. Curti
Longmans, Green and Co.
\$3.20 $5\frac{1}{4} \times 7\frac{3}{4}$; ix + 527 New York

This seems to us a sound and useful book on child psychology. The author holds what we think a well-balanced position on the whole environment-heredity question, which makes her discussion of such problems as the causes of juvenile delinquency of considerable value.



LE SOMMEIL.

By J. Lhermitte *Armand Colin*
10.50 francs (paper)
12 francs (cloth) $4\frac{3}{8} \times 6\frac{3}{4}$; 211 Paris

In this little book Dr. Lhermitte describes the physiological and psychological aspects of sleep.

DE OMNIBUS REBUS ET QUIBUSDEM ALIIS

A CENTURY WITH NORFOLK NAVAL HOSPITAL. 1830-1930. *A Story of the Oldest Naval Hospital, the Medical Department of the Navy and the Progress of Medicine Through the Past One Hundred Years.*
By Richmond C. Holcomb

Printcraft Publishing Co.

\$6.50 6 x 9 $\frac{1}{4}$; 543 Portsmouth, Va.

In this delightful book a former Medical Officer in Command of the Norfolk Naval Hospital turns historian. As is indicated in the subtitle, the book is by no means confined to the history of that institution. The narratives of the yellow fever epidemic of 1855 and of the battle between the *Virginia* and the *Monitor* will be found interesting. In the sketch of the state of medicine in 1830 is quoted a case history of "Paruria Erratica, or Uroplanina," in which urine was discharged by the right and left ears, the left eye, the right and left breasts, and the navel. This is in its way as remarkable a case as that of the birth of Gargantua through his mother's left ear, recorded by the celebrated French physician Rabelais.

FADS, FRAUDS AND PHYSICIANS.
Diagnosis and Treatment of the Doctors' Dilemma.

By T. Swann Harding The Dial Press Inc,
\$3.50 5 $\frac{1}{2}$ x 8 $\frac{1}{8}$; 409 New York

This book will enrage all right-minded medical men, and will be quoted (unfairly) extensively by Christian Scientists and chiropractors. Very little in the present state of medicine, surgery, and pharmacy pleases the author. His documentation, mainly from the files of the professional journals, is extensive and impressive. The book would have been more effective

if the author could have refrained from screaming quite so often.

Actually, of course, all is by no means well in medicine; the doctors themselves are frequently and considerably wrought up about conditions; but when a layman ventures to criticize, even if he merely repeat the remarks of doctors, he may be sure that the faculty will be upon him at once.

The author's remedy is State Medicine. He holds that turning the doctors into job-holders would make everything lovely. His optimism we cannot share.



LO!

By Charles Fort

Claude Kendall

\$2.50 5 $\frac{1}{4}$ x 8; 411 New York

This volume would have pleased Augustus de Morgan. The author holds that the earth is stationary; that the stars are volcanoes in a hollow sphere of land surrounding the earth; that frogs and snails fall in rainstorms; that earthquakes are caused by the appearance of new stars; and a good many other things. He has apparently devoted unlimited time to searching newspaper files for mysterious happenings. Unfortunately he rarely gives an adequate account; his method is one of enumeration of cases, not of analysis. The book will perhaps furnish a half-hour's entertainment.



THE ADVENTURE OF SCIENCE.

By Benjamin Ginzburg Simon and Schuster
\$5.00 6 x 9; xvi + 487 New York

A popular history of science which plays the spot light successfully upon Pythagoras, Aristotle, Archimedes and Ptolemy, Copernicus, Galileo, Harvey, Newton, Lavoisier, Dalton, Faraday and Maxwell, Helmholtz, Lamarck and Darwin, Pasteur, Mendel and Einstein. The

book is well written and makes pleasant and easy reading.



THE GREEK ELEMENT IN ENGLISH WORDS.

By John C. Smock.

Edited by Percy W. Long

The Macmillan Co.

\$15.00 8 $\frac{3}{8}$ x 11 $\frac{1}{2}$; xiv + 356 New York

The desire of the author was to present "a volume of ponderable evidence that the Greek element in the English vocabulary has been underestimated." The evidence weighs 2200 grams. The list includes, we fear, what might be called padding, through the inclusion of Latin and other words with Greek suffixes, as *-ism*, *-ist*, *-ite*, etc.



SCIENCE AND THE SCIENTIFIC MIND

By Leo E. Saidla and Warren E. Gibbs

McGraw-Hill Book Co., Inc.

\$3.00 5 $\frac{1}{2}$ x 8; xiv + 506 New York

A collection of non-technical essays about science and its methods and purposes, designed as a text-book in English composition for students in technical schools. The material seems well chosen; and certainly one can but hope that the students who use the book will acquire some of the literary merits of the models offered them here.



THE ART OF GOOD LIVING. *A Contribution to the Better Understanding of Food and Drink together with a Gastronomic Vocabulary and a Wine Dictionary.*

By André L. Simon Alfred A. Knopf, Inc.

\$2.50 5 $\frac{1}{4}$ x 8; xii + 201 New York

This is a useful addition to gastronomic literature. It contains much sound advice on food and drink, and on what combinations are meritorious. Possibly not a book to recommend to American readers except such as contemplate a trip to regions where the precepts of M. Simon can be more legitimately practiced.



DOCTORS AND SPECIALISTS. *A Medical Revue with a Prologue and a Good Many Scenes.*

By Morris Fishbein

Bobbs-Merrill Co.

\$1.00 5 x 7 $\frac{1}{2}$; xi + 118 Indianapolis

Brief sketches of the various specialties, incorporated in an electuary of puns and wise cracks. The book is dedicated

To

Every Doctor with a Sense of Humor,—
Something a Doctor Must Have to Live at All.

No doubt a sense of humor is an asset to a physician, but we have known some who seemed to get along very prosperously without one.



THE MYSTERIOUS UNIVERSE.

By Sir James Jeans

The Macmillan Co.

\$2.25 5 $\frac{1}{2}$ x 8; ix + 163 New York

Sir James Jeans probably needs no introduction. His books sell in quantity, and for cause. The present small volume, which he describes as a sequel to his former book, *The Universe Around Us*, is distinctly the best exposition of the cosmological bearings of the newer physics which we have seen.

THE QUARTERLY REVIEW of BIOLOGY



THE PRIMATE BASIS OF HUMAN SEXUAL BEHAVIOR

By GERRIT S. MILLER, JR.

United States National Museum, Washington, D. C.

HUMAN sexual behavior is ordinarily regarded as a subject that can be understood from the study of man alone.

More than that, the prevailing practice of investigators, with few exceptions, has been to regard this behavior, alike in its "normal" and "abnormal" aspects, as something specifically human, in the sense of something that differs radically from the behavior of all non-human mammals. To writers who follow this course a full and clear recognition of man's supposedly isolated psychological position has naturally appeared to be the foundation of all sound reasoning about human activities in the domain of sex, whether in the limited field of sex as the determinant of personal conduct or in the broad field of sex as the starting point for the social institutions that have grown up around it.

This belief that human sexual behavior is governed by its own laws was clearly and simply expressed by Thomas (1909, p. 531) in the words: "But as he [man] came into possession of a characteristic human mind . . . he began to make the sexual interest a play interest, and this animals have never done. They have a

pairing season, and man has not." Thomas did not attempt to tell why or how it has been possible for man thus to deviate from the course pursued by other mammals. He was content with having stated the supposed fact of man's unique attitude toward sex. Bronislaw Malinowski, however, has tried to explain this attitude on physiological grounds. In his first study of Trobriand Island family life (1927, pp. 193-201) he thus contrasts the factors that he believes to regulate the behavior of man's nearest mammalian relatives on the one hand and of man himself on the other:

Among apes the courtship begins with a change in the female organism, determined by physiological factors and automatically releasing the sexual response in the male. . . . Mating occurs as the culminating act of courtship and with this the female conceives. With impregnation the rut is over and with its end there ceases the sexual attractiveness of the female. . . . Outside the rutting season the sexual interest is in abeyance and the competition and strife as well as the overpowering absorption in sex are eliminated from the ordinary life of an animal species.

There is nothing in man which acts with the same sharp determination as does the onset of ovulation in any [other] mammalian female. . . . man is ready to make love at any time and woman to respond to him—a condition which, as we all know, does not

simplify human intercourse. . . . The [human] sexual impulse is not confined to any season, not conditioned by any bodily process, and as far as mere physiological forces are concerned, it is there to affect at any moment the life of man and woman . . . : there is no purely biological release mechanism in man; but instead there is a combined psychological and physiological process determined in its temporal, spacial, and formal nature by cultural tradition

The views thus expounded by Thomas and by Malinowski are neither new nor are they peculiar to these two writers. It would probably be futile to try to find when and where they first appeared in print, or to try to catalogue all the authors who have, in one form or another, set them forth. They are, indeed, essentially folk beliefs that originated in the popular mind as the result of uncritical comparisons of the ways of men with the obviously different ways of cattle, goats, sheep, deer, swine, horses, and dogs. And, on the sole basis of these comparisons the generally accepted conclusions appear to be well founded; it is unquestionably true that between human sexual behavior and the corresponding behavior of the most widely known mammals other than man great differences exist. It should not surprise any one, therefore, to find how strongly, even in the technical literature of psychology and anthropology, the idea of man's essential peculiarity is intrenched.

When, however, we cease to compare man's behavior merely with that of domestic ungulates and carnivores or with that of imaginary apes acting like partly humanized dogs, and take the trouble to compare it with the true behavior of mammals in general, we find that there is nothing very exceptional in its nature. In this department of his psychology, exactly as in his anatomy and physiology, man is then seen to occupy a definite and easily understood place among the members of the animal class to which he pertains.

In writing this paper I have had two main purposes: *first* to show as clearly as is now possible how the sexual behavior of man is related to that of other mammals, and *second* to discuss more fully than on a previous occasion (Miller, 1928) some of the social implications that seem to arise from the conditions at present known to exist.

THE MAIN TYPES OF MAMMALIAN SEXUAL BEHAVIOR

That all mammals are not subject to a single, uniform rule of sexual behavior is a commonplace of popular observation. For instance, everyone who has paid attention to the breeding habits of mammals knows that the northern members of the deer tribe, with their conspicuous autumnal rutting season, behave differently from domestic cattle and dogs, in which no season of this kind occurs. Unfortunately, in the field of accurately observed animal psychology our knowledge is still very imperfect. But in spite of this circumstance it now seems possible to recognize that the sexual activities of every species of mammal tend to follow the outline of one or the other of three main patterns of behavior. These three patterns or types, which were recognized in part by Heape (1900), are probably dependent on physiological differences in the production of the chemical substances (hormones) that stimulate sexual activity. For the present, however, they can be most conveniently defined in terms of behavior, as follows:

Type No. 1.—Mating behavior of both sexes limited to short, definitely determined periods that are in most instances seasonal in their occurrence. Examples,—many deer and other (though not all) ungulates, most (perhaps all) pinnipeds, some carnivores, some rodents, some bats, and probably most insectivores.

Type No. 2.—Mating behavior of females limited to short, definitely determined periods that may or may not be seasonal in their occurrence; mating behavior of males not thus limited, but always ready to manifest itself in response to a female in appropriate physiological condition. Examples,—all of our familiar domestic mammals; probably the elephants; many of the ungulates, carnivores and rodents, especially those that live in warm and tropical regions.

Type No. 3.—Mating behavior of neither sex limited to short, definitely determined periods, but nearly always capable of manifesting itself, under favoring circumstances, in healthy adult and subadult individuals. Examples,—most of the primates that have been subjected to adequate study (several species of macaques; one species of baboon; several individuals of chimpanzee, a pair of oranges).

OBSERVATIONS ON THE FIRST TYPE

In *Type No. 1* the psychology of both sexes is, essentially, and so far as the species as a whole is concerned, subordinate to a definite, individual, mating rhythm, presumably determined by the presence of the stimulating hormones, in both sexes, during sharply defined, short periods only. The sexual behavior rhythms of female domestic mammals are well known. That the males of many kinds, among those not made familiar by domestication, follow an equally rigid periodic behavior pattern is not so generally realized. I shall therefore quote accounts of a few conspicuous examples of masculine subjection to rhythm.

Describing the rut of the whitetail deer, Seton (1909, vol. 1, pp. 104, 106) writes:

As October comes on another change sets in with the bucks. Their necks begin to swell and their mating instincts to arouse. Hitherto they have been indifferent to the does when they met by chance,

but now they set out to seek them. . . . As November, the true rutting time, draws near, the necks of the bucks become enormously enlarged. . . . Their whole nature seems to undergo a corresponding change at this time, and by November they are blind and mad with desire, as well as ready and eager to fight any of their own or other kind that seems likely to hinder their search for a mate.

The same author says of the moose at rutting time (1909, vol. 1, p. 169):

The physiological change, called puberty in man, now sets in with the moose. He is subject, indeed, to an annual puberty. At other times he is exempt from the much-mingled pleasures of the fatuous epoch, and free to mind his own business. Early in September the rut sets in, with an exaggeration of everything that is male in his mental, moral, and physical make-up. He devotes all his energies to the matter in hand; he even neglects to eat; his all-dominant object now is to find a mate.

The sexual behavior of the male thirteen-striped ground squirrel is perhaps even more strictly governed by physiological rhythm than that of a male deer, for, while the buck when out of season is merely indifferent to the doe, Otis Wade (1927, p. 270) has observed that the male ground squirrel, after his short period of rut has passed, becomes positively antagonistic to the female. Of the animals that he had under observation Wade writes:

Breeding activities are at their height during the last two weeks of April; however, this varies with the season. Some mating occurs earlier, and undoubtedly some well into May. One observation, which has an important bearing on this point, is that the males are sexually active for only about two to four weeks in the spring, more commonly for two than four weeks. This appears to be the chief factor governing the rutting season for I have observed females on a number of occasions willing to mate, both before and after the males were sexually active—though in more cases afterwards—and in a few instances for some time after the males had lost the rutting impulse. The following will serve as an example: On April 30, a male was put with an "old" female. They soon mated and the male was then segregated. The female did not become pregnant. As soon as the period of gestation [28 days] had

elapsed, she was put with five different males. In every case the female was willing to mate but none of the males was then sexually active and all refused to accept her, but instead were very belligerent and fought viciously when approached by the female in a friendly manner.

Of another North American rodent, the white-tailed prairie-dog, Alfred H. Stockard (1930, p. 473) finds that the males come out of hibernation early in March, to be followed by the females about two weeks later. Sexual activity then "continues within a time limit of two or three weeks for the entire population in a given locality. After this period a rapid decrease in size and content of the sex glands of the males occurs until they are approximately only one tenth of their previous weight." There is only this one breeding season each year.

Probably no example of a special, physiologically determined breeding psychology is more striking than the one presented by the males of the northern furseals (Elliott, 1884). During a great part of the year these seals lead a pelagic existence, their attention given over to the capture of fish. Sexual activities at sea are impossible, as mating can not take place in the water. In May and early June the males of the Alaskan furseal arrive at the Pribilof Islands, where each individual takes up a position on the breeding grounds and fiercely defends it against his rivals, there to await the coming of the females. About the middle of June the females begin to appear. As they land they distribute themselves among the males, in the proportion of from two to fifty—usually from fifteen to twenty—females to each male. The entire energy of the breeding adult males during their stay on land, from early May until about the 10th of August, is given over to the sexual function in its two aspects of battling with other males and impregnating the females. The con-

flicts are most severe during the period when the bulls are establishing themselves on their stations before the arrival of the cows.

Throughout this breeding season of three months or more the digestive function of the males is wholly suspended, and sleep is almost eliminated. Elliott (1884, p. 84) thus pictures the complete absorption of the bulls in the business of sex.

All the bulls, from the very first, that have been able to hold their positions, have not left them from the moment of their landing for a single instant, night or day; nor will they do so until the end of the rutting season, which subsides entirely between the 1st and 10th of August, beginning shortly after the coming of the cows in June. Of necessity, therefore, this causes them to fast, to abstain entirely from food of any kind, or water, for three months at least; and a few of them actually stay out four months, in total abstinence, before going back into the water for the first time after "hauling up" in May; they then return as so many bony shadows of what they were only a few months anteriorly; covered with wounds, abject and spiritless, they laboriously crawl back to the sea to renew a fresh lease of life. Such physical endurance is remarkable enough alone; but it is simply wonderful, when we come to associate this fasting with the unceasing activity, restlessness, and duty devolved upon the bulls as the heads of large families. They do not stagnate like hibernating bears in caves; there is not one torpid breath drawn by them in the whole period of their fast; it is evidently sustained and accomplished by the self-absorption of their own fat, with which they are so liberally supplied when they first come out from the sea and take up their positions on the breeding-grounds, and which gradually disappears, until nothing but the staring hide, protruding tendons and bones mark the limit of their abstinence.

A less highly specialized form of breeding association, based on the same underlying psychology, has recently been described by L. Harrison Matthews as occurring in the elephant seal of South Georgia (1929, pp. 239-240).

Two important circumstances in connection with type No. 1 are, first, that this kind of behavior occurs chiefly in

mammals that are subjected to conspicuous seasonal changes in climate, and, second, that it is usually if not always confined to mammals in which the males have a seasonal rhythm of spermatogenesis. Though we are still ignorant of the exact conditions pertaining to spermatogenesis in the great majority of mammals, we know that in many kinds the production of sperm does not continue uniformly throughout the year. Robert Courrier (1927, p. 176) has summarized the facts in a passage that I translate as follows:

Mammals are divisible into two groups according to their testicular activity. Some have a germinal substance that constantly produces spermatozoa; they have *continuous spermatogenesis*; among them are, for instance: man, guineapig, rabbit, house mouse, rat, dog, cat, boar, horse, etc. The germinal substance of the others is active at certain times only, it is subject to seasonal variations; among these mammals with *periodical spermatogenesis* we find especially such wild animals as the mole, the bats, the European hedgehog, the marmot, the polecat, the weasel, the beech marten, etc.

John R. Baker (1930) recently studied the seasonal variations in the spermatogenesis of British mice of the genera *Apodemus* and *Eutamias*. In *Apodemus* he found that the testis may shrink from a maximum summer weight of over 900 milligrams to a minimum winter weight of less than 50 mg. "There was complete histological dedifferentiation in the minute testes of the winter of 1925-1926. No spermatocytes, spermatids or sperms are found in the tubules. . . . The vesiculae seminales underwent a series of size-changes corresponding with those of the testes, varying from an average of about 10 milligrams in the winter of 1925-1926 to about 400 milligrams in the summers of 1926 and 1927." The corresponding data for *Eutamias* are not explicitly given. Similar observations on southern blue and fin whales have been published by Mackintosh and Wheeler (1929, pp. 405-412) and

on the European common shrew by Middleton (1931).

It is also to be noticed that mammals belonging to families or genera whose usual behavior is of this definitely regulated kind may, either as individuals or as entire species, depart from the general rule, and display behavioral features that belong more properly to type No. 2 or even to type No. 3. Such a variation on the part of a species has been recorded by Blanford. Describing the habits of the axis deer (1888-1891, p. 549) he writes:

"There is, I believe, much variation in the rutting-season. . . . I am under the impression that young fawns are born almost throughout the year. Certainly there is great irregularity as to the period of dropping the horns, and bucks with perfect antlers may be found at all seasons."

Striking individual departures from the usual habits of a species have been observed in the American elk. This animal has an autumnal rutting season like all northern deer. During the rest of the year the sexes, as a whole, appear to be indifferent to each other. O. J. Murie, of the U. S. Biological Survey, who has given several years to a study of the elk herd in the Yellowstone National Park, writes me under date of April 16, 1930:

I have never seen the slightest indication of sexual interest among animals on the winter range or on the feed grounds. I asked Mr. A. P. Nelson, who is in charge of the Elk Refuge, and he has seen no such actions during the years that he has been here. On the other hand I have frequently noticed that old bulls will "shoo" away younger bulls or cows equally from any choice bit of hay he might fancy and I know of at least three instances where a bull killed an adult cow, by puncturing the abdomen with a tine of the antlers.

However, a tame young bull elk kept at the government refuge showed no such limitation of his sexual impulse. In the letter from which I have just quoted Mr. Murie writes of this animal:

I caught him as a new born calf. He was raised on milk, and at the age of a month or so was given the freedom of the place. He is now almost two years old and wanders at will over the Refuge, but prefers to remain near the farm buildings and is perfectly tame and can be petted. Before this animal was seven months old Mr. Nelson saw him many times attempting to mount wild cow elk which wandered into the farm yard and it seems to be a regular habit with him. Last month, March 1930, I saw him mounting a domestic cow.

Seton (1925-1928, vol. 3, p. 43) records the case of a captive bull elk that successfully established sexual relations with a mare and a gelding. Unfortunately he does not give any information as to the adolescent history of this animal. Of even greater interest is a note on the behavior of a bull elk published by Caton (1881, p. 315). It shows that the animal deliberately abandoned females of his own kind for one of a very different species, and also that the sexual potency of this bull continued throughout the period of antler growth. Caton writes:

When I had but one male elk, with several females, a strong attachment grew up between the buck and a two-year old Durham heifer, so that he abandoned the society of the female elk, as the heifer did that of the cows in the same inclosure with which she had been reared, and they devoted themselves exclusively to each other. When they laid down in the shade to ruminate, they were always found close together, and when one got up to feed, the other would immediately follow. They kept away by themselves, always avoiding the society of all the other animals. Whenever the heifer was in season, which occurred quite regularly every month, she accepted the embraces of the elk, without showing an inclination to seek the other cattle; nor did this seem to be the result of any constraint. This intercourse continued throughout the summer, during the entire growth of the antlers of the elk, but unfortunately he was killed before the rut commenced with the female elk.

The American pronghorn, whose sexual behavior, as a species, appears to be strictly of this type No. 1, is also known to show individual peculiarities.

Caton (1881, pp. 45-46) quotes Canfield's account of a young animal in captivity. "When three months old, he commenced to leap upon other pet antelopes, the dogs, young calves, sheep, goats, and even people. . . . He would in this way go at anything held up to him."

OBSERVATIONS ON THE SECOND TYPE

In *Type No. 2* the psychology of the female varies synchronously with an obvious physiological rhythm of the reproductive organs, but that of the male appears to be constant, stimulated, presumably, by a hormone always present throughout the period of sexual maturity. In well marked examples of this type, such as those so widely known in domestic dogs, cattle, sheep, goats, and swine, and as Warner (1927) has carefully studied in the white rat, the female is habitually sexless in her behavior except when she is in heat and not pregnant, but the male is responsive at any time to a female in appropriate condition. Rare instances of sexual behavior during pregnancy have been recorded in the rat by Long and Evans (1922, p. 58) and Nelson (1929); in the house mouse by Crew and Miskaia (1930) and Watt (1931).

A variant of type No. 2 has been described by Stockard and Papanicolaou and by Louttit as occurring in guineapigs. Louttit (1927) found the sexual impulse of the male to be so constantly active that the condition of the female had no specific influence in arousing it. Regardless of their physiological state the females were always sexually attractive to the males; nevertheless the females would not permit intercourse when they were pregnant or when they were not in heat. The males appeared to have no means of knowing when a female was in heat except by trial; and they would lose such a female in a group of others.

Stockard and Papanicolaou (1919, p. 229) say that "a male after long isolation from females becomes sexually excited by the presence of any female irrespective of her sexual condition, and he invariably attempts to copulate." The behavior of this animal would therefore seem to be intermediate between types 2 and 3.

As to its geographical distribution, type No. 2 appears to occur most commonly in warm or tropical countries where seasonal contrasts in climate have much less influence on the general living conditions of animals than is the case in northern regions. Slade (1903) believed this type to be present in the Indian elephant; Roosevelt (1910, p. 110; 1914, vol. 1, p. 382, vol. 2, pp. 585, 604) observed it in the topi, hartebeests, and gazelles of British East Africa; and Schuster (1929, pp. 115-116) has more recently recorded it in the reedbuck, hartebeest and gnu.

OBSERVATIONS ON THE THIRD TYPE

In *Type No. 3* the sexual psychology of the female as well as that of the male has been liberated from strict periodical oestrous control; or, what amounts to the same thing so far as behavior is concerned, the physiological stimuli to mating, though they may be stronger in the female at some times than at others, appear to be rarely if ever completely absent in either sex at any part of the year. The behavior patterns are not necessarily uniform at all seasons; but conspicuously marked physiological rhythms are no longer the nearly exclusive regulating factors in the mating behavior of either sex. Mating behavior becomes established as part of the play activities of young individuals, and from this early period onward until senility makes it impossible, it may occur at any time, even during pregnancy, when not inhibited by some unfavorable factor such as fear, fatigue, hot weather, molt, injury

or ill health. Throughout its course it tends, in both sexes, to assume more nearly the form of an ever-available amusement activity than that of a periodic blind submission to an inescapable racial force. Individual variations of sexual behavior appear to be more common than in types 1 and 2.

This type of sexual psychology has been recorded as occurring in Orangs, Chimpanzees and several Old World monkeys and baboons, all of them tropical or subtropical in distribution.

The literature in which the real sexual behavior of non-human primates has been described is neither very extensive nor does it cover a long period of time. In all, there appear to be only about a score of papers by some sixteen writers. The first appeared in 1914, the last in 1931.

When the details recorded by these observers are fitted together they make a composite picture of sexual behavior in the higher non-human primates that conspicuously differs from the pictures we have just looked at as illustrations of behavior of the first and second types. The main outlines of this new picture have been thus traced by Zuckerman (1930, p. 748):

The matings of the lower mammal are confined to short periods circumscribed by the activity of the follicular hormone. The matings of the primate are diffused over the entire cycle, paralleling the continued action of the follicular hormone, but varying in frequency according to the varying degrees of activity of that hormone.

(a) *Macaques and baboons*

The most complete account of the macaques is the one given by Hamilton (1914). Its main features I have already (1928, pp. 278-279) summarized as follows:

Doctor Hamilton based his observations on twenty subjects, eighteen macaques (*mulatta* and *irus*) and two "baboons" named "Grace" and "Sandy" (ac-

tually, I am convinced, after corresponding with Doctor Hamilton, a female Celebean black ape, *Cynopithecus niger*, and a very large male pig-tailed macaque, *Macaca nemestrina*). The animals were kept part of the time in cages and part of the time in a state of semi-freedom, at a laboratory situated "in the midst of a live oak woods in Montecito, California, about five miles from Santa Barbara." The females were not subject to a psychological oestrous cycle, but were ready to accept the male at all times when not physically incapacitated (as by traumatism or recent parturition). The adult males were sexually attracted by any adolescent or adult female at any time; their sphere of sexual interest was not limited to female individuals of their own kind, but was so widely extended as to include females of other species, also weaker monkeys of the male sex, and animals of the most varied sort (snake, kitten, puppy, fox, human infant, man's hand); autoerotism occurred, but not frequently, the only observed instance being that of a male when temporarily kept in solitary confinement. Homosexuality was most frequent in immature males, least frequent in females. The absence of specific and single release of the sexual impulse was almost as evident in the females as in the males. Among them homosexuality was not absent, though it was far less frequent than in the males; one female went out of her way to establish sexual relations with a male dog, another offered herself to a ranch hand employed about the laboratory. Continuous confinement of one male with one female resulted in a marked diminution of sexual enthusiasm in both, particularly in the male; a condition that the animals sought to remedy by special stimulations often sadistic on the part of the male; vigor was immediately restored by supplying each with a new mate. Females and immature males deliberately employed sexual artifice either to bring enemies within reach of attack or to turn aside the aggressions of stronger animals. Sexual jealousy was well developed in both males and females.

Unlike the monkeys observed by Hamilton those studied by Kempf (1917) were kept under unnatural environmental conditions in cages. Of the six subjects all were *Macaca mulatta* (= "*rhesus*") and all but one were males. The female was immature and was less sexually attractive to the males than the individuals of their own sex. Hence the observations bear mostly on homosexuality. No period of heat was observed in the female; and nothing in the

entire paper gives the slightest support to the idea that sexual response in a healthy male monkey is ever in abeyance. One male is described as conspicuously algolagnic.

Objections are frequently brought against research based on animals kept under unnatural conditions, but these objections mostly arise from the confusing of two different things, namely, the study of psychological reaction patterns and the study of the behavior of a species in nature. Laboratory surroundings provide unfamiliar stimuli and give inadequate information about activities in the wild; but it has yet to be shown that these stimuli are capable of doing anything else than to reveal the reaction patterns normal to the animal under investigation. The longest continued of all laboratory experiments, domestication, has not obliterated the essential psychological differences between horse and cow or between dog and cat. The unlike sexual traits of caged macaques and caged microtine rodents, which breed with equal freedom in captivity, cannot be attributed to unnatural surroundings, because these surroundings for both animals are alike.

Hartman's observations on *Macaca mulatta* (= "*rhesus*") are in accord with those of Hamilton. In his first paper (1928, p. 185) he writes: "as a rule the females will accept the male whenever given the opportunity . . . the stage of the menstrual cycle has nothing to do with their refusal or acceptance." In his second paper (1931, pp. 136, 138-139) he gives a particularly interesting account of the depressive influence that adverse climatic and physiologic factors exercise on sexual behavior:

In the first place, the heat of summer is unfavorable to the monkey, at least to the tropical monkey. This is well known to animal importers and hunters. We find it so in the Carnegie Colony. By far the greater

number of deaths have occurred in the summer and fall months even among the "acclimated" individuals, though the death rate has been cut down since we have ameliorated the heat conditions by using a fine spray of water or "artificial mist" in the paddocks. The animals are more likely to lose weight in the summer, and they then shed their hair, which further exaggerates their unprepossessing appearance at this time. Menstruation is more irregular in summer, often absent entirely; moreover the sexes are far less interested in each other and the usually quite willing males may occasionally even entirely refuse to copulate. . . . The low ebb of sexual activity in the Carnegie Colony in the summer months is therefore incontrovertible and the sterility of the animals is due to the absence of an ovulatory cycle, although menstruation continues. That the males are not sterile is shown by the repeated recovery of motile sperms from mated females and by a single conception on July 24 in a favorable female. Yet the males are less ardent in summer than in winter and refuse mating with some females altogether.

In his account of the self-mutilation of a male *Macaca mulatta* (= "*rhesus*") Tinklepaugh (1928) describes a case of monogamous attachment on the part of a young monkey, "Cupid," to the older female, "Psyche," (of another species, *M. irus* = "*cynomolgus*") that had sexually initiated him. So strong was this attachment that "Cupid" behaved with the utmost unfriendliness toward other females (of his own kind) with which he was brought in contact. It was only after a long course of "conditioning" that he could be made to accept them sexually; and, to all appearances, this treatment resulted in disturbing his mental balance to such a degree that finally, on being led between the cages containing the different females, he mutilated himself by inflicting, with his long canine teeth, no less than twenty severe lacerations on his legs, genitals and tail.

The baboons studied by Gear (1926) were five females and a male, all identified as *Papio porcarius*. The author writes:

During the dioestrus and metoestrus periods the behaviour of the baboons shows all the liveliness and

vigour characteristic of the primates. They are continually on the alert, showing a restless interest in their toilet, their food, and their environment. Though the baboons were always on friendly terms with each other, yet, at dioestrus and metoestrus, the females would not tolerate any sexual advances of the male. During the period of the genital enlargement, however, a marked change in behaviour occurs. . . . In the females under observation, it was at this time that they permitted and even solicited the advances of the male, resulting in frequent acts of coitus." His conclusion is that the [female] baboon shows a typical phase of desire occurring during the engorgement of the external genitalia.

These observations are partly confirmed by Zuckerman, who, however, found that the female hamadryas baboon will accept the male at other times than those of genital enlargement. Writing of the animals in the London Zoological Gardens he says (1930, pp. 729-730):

On "Monkey Hill," where a colony of hamadryas baboons of both sexes and all ages lives, it is possible to observe the behavior manifestations of the sexual skin cycle under relatively "natural" conditions. The bond between a male and his female is closest when there is greatest pudendal swelling. . . . Copulation is most frequent during the stage of perineal enlargement, though it also occurs during the quiescent phase. When more than one female is owned by a male, priority in the harem is taken by the female "in oestrus." Under such circumstances the male overlord copulates almost entirely with the female who is in the phase of pudendal enlargement. I have never observed the male mating at such a time with a second female of the harem who is in the quiescent phase. . . . The instances of "infidelity" which I have noted have involved only the quiescent female, never the "oestrous" female.

In an earlier paper (1929, pp. 86-87) he gave the following more detailed account of the social system that prevails among the hamadryas baboons:

The more or less recent establishment of colonies of Hamadryas baboons in many European Zoological Gardens has provided excellent opportunity for careful study of the social relationships of these monkeys under conditions approaching their natural environment as closely as is possible in a state of captivity.

These relations are in no way subjected to human interference. Observations made in London and Munich have shown that the internal arrangements of such colonies are always the same. Their more prominent features, without entering into detail, are as follows.

Each colony consists of harems, bachelors, and children. The individual harems never come into close contact with each other, and certain of them are more inclined to keep away from the main body than others. The "married" males in all cases dominate the "bachelors" who will invariably move away from any favourable spot in which they may be, on the approach of a harem.

Females are completely dominated by their males, following them wherever they go. The bond between male and female is, however, closest when the latter is "in oestrus." At such time the female hardly ever moves from the male's side, whereas in the quiescent phase she may sit several feet away from him. When more than one female is owned by a male, priority in the harem is taken by the female "in oestrus."

In some instances a male will follow readily where his female leads; in others, if a female wishes to move, or to remain where she is, against the male's desire, she attempts to get her way through sexual approach. Both sexes of all ages appear to present themselves sexually to those of their fellows whom they fear; this appears to be a means of diverting assaults.

All baboons manifest homosexual tendencies. Amongst males this type of response is most frequent amongst the "bachelors," though married males occasionally have homosexual relations, generally with "bachelors," and very rarely with each other. There is less homosexuality amongst females, and what there is is restricted to the members of the same harem.

Writing on the breeding season of non-human primates Zuckerman concludes (1931, p. 339) that such records as he has been able to tabulate "indicate clearly that monkeys can conceive at any time in captivity, and presumably, therefore, like the baboon, at any time in the wild." His field observations "prove conclusively that the chacma baboon of the Eastern Province of South Africa has no demarcated breeding season in its wild state" (p. 341).

(b) Great Apes

Turning next to the recent accounts of the great apes we find that no less variety of sexual behavior has been recorded, and that the studies, especially those of chimpanzees and of the gorilla "Congo," have been made with particular care and in great detail.

Montané (1915, 1928) appears to have been the first to observe a female chimpanzee that was ready to respond to the sexual advances of the male "frequently" and "at any moment," throughout pregnancy as well as at other times. Sokolowsky (1923) remarks that a large adult male chimpanzee confined in a cage with several females and a young male practiced "repeated intercourse every day with his females," and that when a female was unwilling the male would use bullying methods to obtain her consent. Köhler (1925, pp. 313-315), although he admits that he was not "able to obtain any adequate notion of the sexual behavior of chimpanzees," made, nevertheless, some very important observations, among them the following:

It seems to me that among these creatures sexual excitement is less specific, and less differentiated from any other kind of excitement, than among human beings. We may almost say that any strong emotion, and thus also any strong external stimulus tends to react directly upon both the colon and the genitals, but not so as to give the impression of exaggerated and concentrated sexuality, but rather of an extreme vehemence and interdependence of all vivid inner processes. We may even say that this extreme frequency of sexual effects implies a certain trivialization of this sphere of life, rather than its intensity. . . . The female of the species definitely menstruates, at intervals of thirty to thirty-one days, and always for a period of between three and six days. During the flow her sexual instinct is absolutely quiescent, but her temper is often particularly amiable. After the cessation of the flow, there is an access of sexual desire, accompanied by a pronounced swelling of the whole external genitalia. At this time the animals

are irritable and uncertain in temper, and suffer a good deal from the very sensitive swollen area, until it subsides.

Passemard (1927) records the algolagnic attack of a male on a female, sexual interest on the part of this same old male in an unripe female, and the seemingly definite stimulation of another male by the sight of a particular woman. Fox (1929, p. 50) made observations on a pair of adult chimpanzees in Philadelphia that rather nearly coincide with those of Köhler. He writes:

Although the act was practiced frequently, day and night, during the interval between the heat periods, it was more prolonged and apparently more interesting to both animals, the female especially, during these periods. 'Heat period' means the duration of the perineal swelling [of the female]. The greater the swelling the more frequent the sexual act.

That the sexual behavior of the orang is equally free from oestrous limitation there can be little doubt. Fox says of the adult male and female in Philadelphia: "The act is practiced daily, without relation to the sexual cycle" (1929, p. 41). His account of the position assumed by the pairing animals is especially important because it appears to be the first record of female passivity during copulation in any non-human primate. Fox writes (1929, p. 41):

The copulatory act of our orangs is worthy of description because of its dissimilarity from that described for the chimpanzee. When the desire animates the male and is reciprocated by the female, he pushes and mauls her a little, whereupon she lies upon her back on the floor. The male then approaches her and separates her legs. During the act he remains in a sitting or crouching attitude and though they are face to face, he does not lie upon the abdomen of the female. The male will sometimes grasp a leg of the female and hold it up and to the side during the conjugation. During the act, there is no fondling, nor do they mouth each other either before or after the act. The female lies passive and often has a hand over her face.

In this connection the observations of Basedown (1927, pp. 151-154) on Austra-

lians, and Malinowski (1929, pp. 336-337) on Trobriand Islanders are of interest. Possibly the habit recorded by Fox is exceptional, as Paul Eipper (1929, p. 78) and Zedtwitz (1930, p. 285) have described postures in which both orangs were suspended by their hands from the bars at the top of the cage. G. Brandes (1930), however, gives observations on two pairs whose behavior almost exactly coincided with that recorded by Fox. One of the males is described as pulling his female about on the floor exactly as a man would handle a sack of potatoes. This does not necessarily indicate that the female orang is at the mercy of the male, as Zedtwitz (1931, p. 14) mentions an unsuccessful attempt by a male to "force" his mate.

As regards the gorilla we still lack observations on adult animals and on males. Yerkes (1927, pp. 520-522) has described the beginnings of sexual behavior in the young female "Congo." At an age believed to be about six years she began sex play with two dogs, a male and a female. The gorilla assumed the active part in this play, and the dogs were always either indifferent to it or annoyed by it. A year later she behaved in a similar and even more unmistakable manner toward men. "Her insistence on sexual contact," Yerkes writes (1928, p. 69), "was extremely embarrassing to us and somewhat dangerous because of her enormous strength, but throughout the period of observation she was unusually gentle and friendly, although determined in her efforts to satisfy her desire."

The gradual development of specifically sexual behavior out of the generalized activities of four young chimpanzees (two males and two females) has been carefully studied by Bingham (1928). Some of the more important of his observations are as follows:

The behavior of these young chimpanzees prior to December 10, 1925, included varieties of social adjustment having, to all appearances, no immediate sexual significance. In these adjustments, however, there appeared components of behavior which differ little, if at all, when appropriately united, from essential adjustments involved in copulatory relations. What appeared to be a new synthesis of responses was observed for the first time on December 10 and recognized as copulatory play. It seemed to involve no new elements in behavior although the adjustment as a whole was novel. Existing factors, previously expressed and developed as parts of other syntheses of responses, appeared to undergo reorganization while I looked on and witnessed initial adjustments of a copulatory nature (p. 78). . . . These young animals merely repeated over and over the copulatory adjustments without copulation. The relations, it seems to me, may quite properly be termed copulatory play (p. 97). . . . Repeated observations involving both males have convinced me that sexual manifestations are asserted in situations which elicit various kinds of excitement, including both agreeable and disagreeable experiences (p. 92). . . . This copulatory play, years before reproductive maturity, is the most surprising behavior I have ever observed! There was remarkable cooperation between the pair. The functional adequacy of their behavior is astounding. . . . I never expected to see such pre-adolescent behavior. Moreover, I am surprised at the front to front position. So far as I know, the lying, ventroventral position in the anthropoids has never been reported (p. 85). . . . Presently they took the standing position of quadrupeds (p. 86). . . . Following the initiation of mutual sex play, there were many repetitions and variations. Conspicuous differences appeared in ventroventral and dorsoventral adjustments. Other variations of significance were noticeable in the social situations that fostered copulatory play. Moreover, the variability that occurred in the sexual behavior itself appeared to be only a continuation of that which prevailed in the sources of such behavior. A heterogeneous group of variable activities, including both primitive responses and recent acquisitions, seemed to contribute in varying degrees to these sexual foci. Excitement—revealed by romping, teasing, petting, fleeing, eating, fighting, tantrums, and commonly by mixtures of these and other activities—was a consistent forerunner of sexual responses (pp. 155-156).

Bingham describes instances of exhibitionism of both types, namely, presentation of the sexual parts to visitors (pp. 131-135) and copulation incited by the

approach of a visitor (pp. 14-17). The former was observed in chimpanzees of both sexes, and in a female gibbon; the latter was noticed in a pair of baboons and a pair of Celebean black apes. I have seen it in a pair of Barbary apes at the National Zoological Park, Washington.

In chimpanzees of both sexes he found masturbatory behavior well developed (pp. 139-151) and involving many different objects, such as hands (both sexes), toes (males), packing boxes (both sexes), measuring plane (male), a kiddy kar (male), mango fruit (female), leaves, small sticks and pebbles (female), pool ball (female) and combination of leaf and bars of cage (female). Passemard (1927) records it in the male chimpanzee that he believed to be sexually stimulated by the sight of a blond servant girl. My observation of the adult male chimpanzee in the National Zoological Park leads me to believe that, when thus engaged, he is indifferent to the visitors of both sexes near his cage. I have, however, repeatedly seen behavior of this kind directed toward adult visitors by a male drill and toward small children by a male Celebean macaque (*Magus maurus*), though in neither case with any apparent regard to sex.

(c) *American Monkeys*

In contrast to these rather full accounts of the sexual activities of Old World primates we find that very little has yet been recorded about the American monkeys. The only carefully made study that I have seen is the one pertaining to the common marmosets kept in captivity by Lucas, Hume, and Smith. About these animals the authors write as follows (1927, pp. 449-450):

On March 23rd [1926] coitus was observed, and also on the next two or three days. Then attempts became fewer and less acceptable to the female, and finally ceased altogether. During the ensuing months

there were no signs of oestrus, and when the young male was at liberty he paid no more attention to the female, through the bars of the cage, than he did to the other male. . . . The night of August 19-20 twins were born. . . . Pairing had again been observed on September 16th, 1926, and on February 4th, 1927, another pair of twins was born. . . .

Miss Hume added, in a note published by Zuckerman (1930, p. 736), "that the time that elapses after parturition before a female will pair is variable. It has been observed after 23, 34, and 45 days. After a miscarriage only 12 days elapsed."

So far as these records are concerned it appears that the mating behavior of the common marmoset differs widely from that of the Old World primates whose habits have been carefully studied, and follows the pattern of type No. 2. It will be interesting to learn whether or not this type of behavior is widely prevalent among American monkeys, and also whether or not it occurs among the lemurs, about whose breeding activities I have been unable to obtain any information.

THE CLASSIFICATION OF HUMAN SEXUAL BEHAVIOR

It is obvious that human sexual behavior has little in common with behavior of the kinds that I have grouped under types 1 and 2. Among the animals that normally conform with these types, some individuals occasionally depart from the usual way of the species in a manner that parallels certain varieties of human activity; but among men and women we look in vain for tribes or individuals that normally or abnormally comport themselves, in affairs of sex, after the manner of deer and fursel or of cattle and dogs. That is to say, we do not find groups of people or even unusual persons of either sex whose sexual impulse lies essentially dormant throughout most of the year to awaken only during a short, seasonally determined, and exces-

sively violent period of rut, or whose sexual activities, if not thus seasonally limited, are, nevertheless, restricted to short periods determined by recurrent physiological cycles in one or the other sex. The facts that have been recorded concerning seasonal periodicity in the sexual behavior of man seem chiefly to concern instances of recurring erotic festivals and slight but recognizable fluctuations in the birth rate (see Heape, 1900, pp. 34-38; Ellis in Moll, 1912, pp. 185-186). Tardieu, however, found a rather striking seasonal variation in the frequency of sexual assault in France, where, through a period of twelve years there were 4194 recorded cases during the months of May, June and July, as contrasted with only 2007 during November, December and January (1878, p. 23). But these human phenomena, like the falling off of sexual activity in macaques under the depressive influence of molt and hot summer weather (Hartman, 1931) appear to be reflections of seasonal changes in climate or in food supply or in other conditions that affect the general state of vital energy rather than strict behavioral reflections of physiological rhythms. On the other hand, when the sexual behavior of mankind is compared with that of non-human members of the order Primates, the natural group of mammals to which man pertains, the discrepancies vanish. To realize this the reader has merely to peruse the foregoing summary of laboratory findings and mentally translate the details into terms of human activities in the field of sex.

Perhaps the psychological rhythms noted by Gear (1926) and Zuckerman (1930) in baboons and by Köhler (1925) and Fox (1929) in chimpanzees, as well as the female aggressiveness described by Tinklepaugh (1928) in a macaque and by Yerkes (1928) in a gorilla may at first

appear unusual when viewed from the accustomed human standpoint. But when these observations are considered in connection with what is known of psychological rhythm in women (see, for instance, Davis, 1926; Ellis, 1928, pp. 213-236; Hamilton, 1929, pp. 196-197) they lose their strangeness; and when the macaque "Psyche" and the gorilla "Congo" are placed side by side with Retif de la Bretonne's Marie and Nannette (1883, vol. 1, pp. 52, 106-107) or Rousseau's Madame de Warens (1914, vol. 1, pp. 313-319) the action of these animals at once becomes humanly comprehensible. Tardieu (1878, pp. 65-71) and Ellis (1904, pp. 173-179) have, moreover, fully recognized the aggressive phase of human female behavior; Hamilton (1929, p. 349) has reported that in the cases of 14 among the 100 men whose histories he studied it was the women who took the initiative in the first sexual experience. Furthermore, it is to be remembered that the physiological rhythms of the female primates under discussion do not set the sharp limits on sexual behavior that we see in mammals of types 1 and 2. Even Zuckerman, who lays much stress on the importance of these rhythms, recognizes that their influence on behavior is only partial. He writes (1930, p. 749): "Monkeys that copulate in captivity do so at all times, but copulation occurs most frequently during the period of maximum sexual skin activity."

More important, perhaps, than any single one of these points of agreement is the fact that although the sexual activities of nonhuman primates have been carefully studied during less than two decades and in a relatively small number of species, they furnish a picture that almost covers the entire field of sexual behavior in man. This generalized-primate picture contains all of the "normal" elements of human behavior that are supposed, both popu-

larly and by many technical writers, to distinguish man from other mammals. It also contains the more conspicuous of the elements that, because they run counter to social conventions, are usually designated as "abnormal" or "contrary to nature." Finally and very significantly, it includes few if any important features that lack some counterpart in the behavior of man.

We are therefore forced to conclude that human sexual behavior is not something isolated and unique. It is merely a common type of primate sexual behavior with a few specialized characteristics, exactly as the human body is a primate body specialized along particular lines. Attempts to understand it without taking into account the psychology of all primates must therefore be as futile as attempts to understand human anatomy without dissecting any other creature than man.

THE SPECIALIZED ELEMENTS IN HUMAN SEXUAL BEHAVIOR

Having now seen something of the points of agreement between human sexual behavior and the corresponding behavior of several non-human primates we may turn to the points of difference. Immediately we are struck by a significant circumstance. Whereas the points of agreement pertain, almost without exception, to elements of fundamental biological importance, most of the points of difference are of a nature that makes their existence, or at least their exact form, depend chiefly on human culture.

Such human behavior patterns as the various forms of clothing fetishism probably have no real homologues in the behavior of non-human primates, and the same is probably true of fetishism with regard to parts of the body; all appear to be dependent on the human habits of wearing clothes and of artificially modifying

sundry physical traits. Nevertheless the distinctly sex-tinged emotional attitude of monkeys toward the process of cleaning each other's fur and skin has been noticed by Zuckerman (1929, p. 78), while Tinklepaugh (1931, p. 430) has recorded a case of persistent modification of a female macaque's facial appearance by hair plucking done by her mate. From such beginnings the human "aberration" might arise. Even more strictly cultural in its nature is conism or transvestism, where the unusual behavior is associated with a highly specialized convention in dress. Narcissism and pyrolagnia are other human peculiarities that seem to owe their being to conditions built up by man himself. The same is true of necrolagnia and psycholagnia. Certainly nothing could appear more unlikely than the origin of pyrolagnia and narcissism among creatures not provided with fire and mirrors; while the development of necrolagnia, undinism and coprolagnia among animals whose mental attitude toward death and the excretory functions is no more complicated than it is in the monkeys and great apes seems almost equally improbable. Bingham, however, (1928, p. 140) reports that he has observed erection reflexes in female chimpanzees after urination and defecation, and Hamilton (1928, p. 304-305) has described rudimentary anal eroticism in monkeys; while Köhler (1925, pp. 83-84, 309-310) gives an account of emotional elements in the reactions of chimpanzees to their own excrement.

Another specialized human mode of behavior has been described under the name of kleptolagny (Kiernan, 1917; Ellis, 1928, pp. 477-491). In its fully developed form this behavior would certainly depend on the human high regard for personal property, the violating of which would furnish the emotional stimulus that in rare indi-

vidual cases might overflow into the sexual sphere. Nothing of exactly this kind has been recorded of any non-human primate; but a personal observation seems to furnish a definite analogy. A half grown baboon (*Papio cynocephalus*) in the National Zoological Park succeeded (February 20, 1930), after long effort, in removing the baseboard from the front of his cage and dropping it on the floor. As soon as the keeper came to replace the board the baboon resisted strenuously, pushing the board away with hands and feet. At the same time he developed a full erection that did not subside until the board was securely fastened back in place and another keeper had arrived with food. In this animal, as in the kleptolagnic shop lifter, mischief and sex went hand in hand.

Masochism deliberately resorted to as a means of sexual gratification is not mentioned in any of the accounts of non-human primates that I have seen. Nor have I noticed any suggestion of it among the primates in the National Zoological Park. Doctor Bingham's remark (1928, p. 92) that sexual manifestations are sometimes asserted in situations that include disagreeable experiences seems, however, to point to its germ.

Psychological hermaphroditism appears to be equally common in man and in all the non-human primates that have been adequately studied. It is known to occur in other mammals; but there is little doubt that it reaches its highest development among the primates, and that when he indulges in this type of behavior, man is merely acting in accordance with one of the normal rules of his order. Complete homosexuality is, however, so far as can now be judged, a special human exaggeration of this widely prevalent primate tendency. On this subject Bloch (1908, p. 530) expressed the extreme opinion that

Original, congenital, enduring homosexuality would appear to be an exclusively human peculiarity. It is very doubtful whether a similar condition exists among animals. We recognize among the lower animals homosexual acts, but no homosexuality. Thus we have no phylogenetic starting-point for the explanation of homosexuality.

More recently William J. Robinson has written (1929, p. 383):

Moreover, this particular perversion is not found strictly speaking among the lower animals, as is the case with most other perversions of the sexual instinct. Of course, homosexual acts have been observed in the life of various animals, but these have been isolated instances, nothing habitual, nothing to justify the conclusion that homosexuality or inversion is an established custom among them. P. Naecke has studied pederasty in animals. The literature on pederasty and tribadism among animals has been analyzed by Karch. The observations of these writers strengthen the conclusion that such perversions are incidental occurrences among animals and that true inversion, as a more or less permanent state, such as is found in man, is peculiar to the human race only.

It is obviously an exaggeration to deny any phylogenetic starting point for the extreme condition met with in man, because there is strong evidence in favor of the view that adult human homosexuality often results from the fixation, by cultural influences, of behavior patterns that are common to young primates of several kinds, man included, and that would tend, under natural conditions, to be superseded by heterosexual behavior after puberty (see especially Hamilton, 1925, pp. 153, 301, 306-307). Nevertheless there is no doubt that permanent adult homosexuality in other mammals is excessively rare, though a case somewhat approaching this condition in a bull is recorded by Seton (1927, vol. 3, p. 43). The only behavior even remotely suggesting it that I have seen in a non-human primate is that displayed by two female sooty mangabeys (*Cercocebus fuliginosus*) now living (1931) in

the National Zoological Park. These animals have been confined together for about ten years. When received they were nearly full-grown. They frequently indulge in homosexual play. On the sole occasion when a male was placed in their cage they took no sexual interest in him but attacked him so viciously that for his safety he had to be removed. Quite probably, however, this was merely a case of resentment against an intruder in the home.

The foregoing types of special human behavior are, it will be easily seen, of no very great biological or social significance. We finally come to two that are more important.

The first of these is that in man there appears to be a stronger tendency than in other primates for the members of a pair to become "conditioned" to each other in such a manner as to lead to long association of an exclusive or mostly exclusive kind. This tendency, which seems to form the basis of the complex sentiment defined by McDougall (1923, p. 425 and 1926, pp. 162, 560) as "tender passion" or "sex love," is known to be highly developed in a few birds, of which the domestic pigeon is a familiar example. Among mammals, however, it cannot be regarded as definitely proved to be common, because many of the supposed cases of natural monogamy rest on such anecdotal, uncritical evidence that they can not be accepted as free from a large element of doubt. Even the best attested instances, like some of those reported in carnivores, may depend on sparseness of population rather than on habit or instinct. Certainly, among mammals there is no known example of a monogamous species comparable with that which we see in the domestic pigeon. And it may be declared with equal confidence that no other primate has yet been shown by properly con-

ducted observations to form, habitually, such lasting attachments between sexual partners as those that are not uncommon in man. As to the behavior of wild primates we have, to guide our opinions, nothing more than field records of pairs or family groups seen together on particular occasions; we know nothing of the duration of such groups. In favor of the view that some non-human primates form at least temporary sexual alliances we have, however, Kempf's (1917), Bingham's (1928) and Zuckerman's (1929 and 1930) significant records of individual dominance and favoritism, and Tinklepaugh's (1928) observation of the strong attachment of a young male macaque to an older female.

The second socially important peculiar feature of human sexual behavior is that man alone of all primates, and probably of all mammals, possesses both the psychological and physical specializations needed to establish the recognized and always present possibility of rape. Even granting that rape may take place, on rare occasions, in other mammals, its essentially human character seems to be beyond serious doubt. Rape may be regarded as a by-product of human ingenuity seconded by the upright human posture with its specifically human remodeling of the primate pelvic region. This remodeling has brought the vaginal orifice into a position relative to the adjacent parts that renders sexual intercourse possible with a resisting or unconscious female forced to lie—or lying helpless—on her back. In quadrupedal and imperfectly bipedal mammals this orifice is so placed that the female voluntarily cooperates with the male in order to effect conjunction of the sexual organs. Except in man, aided by superior intelligence and favorable anatomy, unconsciousness or active resistance on the part of the female normally renders the sexual

act impossible. The monkeys studied by Hamilton (1914) and Kempf (1917), as well as the chimpanzees observed by Montané (1915, 1928), Passemard (1927), Bingham (1928) and Fox (1929) presented no exception to this rule. The same was true of a pair of gibbons (*Hylobates leucogenys*) recently living in the National Zoological Park. During copulation both animals hung suspended by their hands from the bars at the top of the cage. The male approached the female from behind, and she, if in responsive mood, remained stationary and raised her knees, while the male curled his pelvis under hers but never grasped her in any way. The female then disengaged one hand (apparently always the left) and, passing her free arm back of the male's neck and body, voluntarily established the required intimate contact. If not responsive the female simply continued to "brachiate" and to pay no attention to the solicitations of the male. According to the keepers copulation continued uninterruptedly throughout a pregnancy that terminated December 27, 1930, in the birth of a healthy infant.

Attempts at sexual coercion on the part of non-human male primates have been recorded by several observers; but this procedure has not been seen to lead to the desired result unless it first induced the victim to cooperate. No instance of actual rape in the sense of copulation forced on a vigorously resisting female appears in any of the published accounts of laboratory observations. Nevertheless, the not infrequently observed attempts at forceful methods, added to the partial adjustments to the ventroventral posture in young chimpanzees as described by Bingham (1928), and the passive behavior of female orangs as recorded by Fox (1929) and Brandes (1930) appear to supply the rudimentary adjustments needed for leading to the specifically human elimination

female consent as a necessary part of the sexual act.

THE SOCIAL IMPLICATIONS

The great importance of comparative psychology in explaining the origin of some of the human behavior patterns that have influenced social development has been particularly emphasized by Kempf. His conclusions (1917, pp. 153-154) seem worthy of quotation almost in full.

In the infrahuman primates as well as in the genus *Homo*, homosexual interests predominate and normally precede heterosexual interests until the adult stage is well established. Homosexual interests occur in both sexes but are more common in the male.

The acquisition of an adequate sexual object for the affective cravings promptly proceeds if it is not inhibited by fear.

The transfer of the affective cravings from a homosexual type of object to a heterosexual object is a very delicate biological procedure and one that must not be inhibited by fear.

Reversion to homosexuality in isolated groups of males or females, such as prisoners, soldiers and sailors, normally occurs if adequate outlets for sublimation are not provided.

Submission as a homosexual object is implicated with biological inferiority in the infrahuman primate. This is probably the phylogenetic root of man's conscious, ineradicable recognition of homosexuality as a biological deficiency.

In the infrahuman primate as in man, sexual submission is practiced in order to procure food (clothing), and protection.

Catatonic adaptations are reflexly practiced by the infrahuman primates as well as by the human primate as a defense.

Vicious, diverting counter-attacks upon an inoffensive object are used for defensive purposes by monkeys. This is in principle comparable to the persistent, systematized counter-attack of the paranoid type of psychotic as a defense to avoid consciousness of his biological deficiencies which persecute him.

The infrahuman primate tends to adopt a variety of animals that do not cause fear, for his sexual cravings; a step preceding the permanent adoption of animals for his affective cravings by primitive man. This principle, of sexual substitution, was probably the foundation of that tremendously important step in man's biological career, namely the subjugation of herds, packs and flocks.

The phylogenetic constitution of man, as we find it completely exposed in the infrahuman primate, ob-
sesses him with what he feels to be perverse tendencies as he strives to behave in an ideally civilized manner and plunges him into the depths of despair when he fails.

It should now be evident that the more conspicuous among those human forms of sexual behavior that are usually regarded as "abnormal" or "contrary to nature" are nothing more than little if at all modified aspects of traits so widely prevalent among primates that they must be recognized as parts of the racial heritage of every member of the order. This is particularly true of autosexuality, homosexuality, zoophilia, and active algolagnia, all of which have been frequently observed in laboratory animals. Bingham, as we have seen, has discovered in chimpanzees the tendencies that may easily represent the beginnings of passive algolagnia. In these directions man has done little more than specially cultivate a few elements of his primate patrimony, without producing anything essentially new; though a few somewhat unimportant human behavior patterns such as eonism, fetishism, kleptolagnia, narcissism, and pyrolagnia appear to stand rather specifically to his credit.

Any one of these socially condemned peculiarities may be of great and sometimes tragic importance to the man or woman that possesses it; but there is no reason to believe that all of them together have had much influence on cultural evolution. When, however, we turn to the admittedly "normal" elements of human sexual behavior we find at least four that seem likely to have taken very significant parts in determining the exact forms of many social institutions.

The *first* and most fundamental of these "normal" elements is the circumstance that human mating activities belong un-

equivocally to type No. 3. These activities, therefore, just as in most other primates whose sexual psychology is known, are practically always ready to manifest themselves, that is to say, they are never the abject slaves of seasonal and physiological rhythms that they are in mammals whose behavior follows the patterns made familiar by deer and dogs.

The *second* "normal" element is the human exaggeration of the tendency to form continuing associations between sexual partners. Hamilton, Kempf, Bingham, Tinklepaugh, and Zuckerman have described numerous imperfect examples of this tendency as displayed by monkeys and great apes. Its variability and capriciousness as we find it in man are well known; but it appears to be, nevertheless, sufficiently prevalent and well enough developed to have acted as an effective social force.

The *third* "normal" element is a trait that man and some other primates possess in sharp contrast with mammals whose sexual behavior conforms with type No. 1 or type No. 2, in both of which, on account of the shortness and violence of the sexual seasons, there is little if any possibility that it could ever become highly developed. (Lataste, however, 1886, p. 400, has recorded a trace of it in a male gerbil.) As a social force it is directly opposed to the permanent mating tendency. Kempf has described it so well that I shall again quote from him (1917, pp. 142-143).

Sexual indifference may result . . . from fatigue of the sexual sensorimotor system through excessive stimulation by a too constant object. . . . Hamilton has . . . reported that monkeys, when they are sexually semifatigued, expose their erotogenic receptors to intensive stimulation of an adequate nature before copulation recurs, and yet the same monkey in such a condition of sexual indifference to his companion, if allowed to have another mate, may rush into a sexual embrace with great excitement and

without previous stimulation; apparently reacting to the new stimulation of his distance receptors. Similar behavior also occurs in man. . . . Perhaps no other feature of the constitution of man has caused so much social turmoil and self-imposed distress as this phylogenetic predisposition of his affective-sensorimotor system. He likes to think of it as an impersonal thing and calls it the work of the devil, evil, immorality, the result of the sins of Adam and Eve, the wickedness of the flesh, and threatens his unruly neurones with the pains of hell fire and even castration. Hatred, anxiety, divorces, insanity, suicides, murders and social ruination commonly result from the conflicts with this phylogenetic predisposition of erotogenesis.

The *fourth* "normal" element is the human male's ability to force his female to accept a mating against her will or when she is unconscious. In every other mammal whose breeding habits have been properly studied the final act of mating depends on the consent of the female; without this consent and the cooperation that goes with it, the male cannot carry out his purpose, no matter if, as in the fur-seals, he may exceed his female six times in weight and incalculably in strength. Several carefully observed examples of female control of the sexual decision have been given in the course of this paper (pp. 384, 387, 389 and 395); others were described by Lataste, 1886-1889 (four species of gerbil, house mouse, Norway rat, guineapig); while additional instances have been more recently recorded by Heape, 1905 (rabbit), Svihla, 1930 (red-backed mouse), and 1931 (Texas rice rat), Svihla and Svihla, 1931 (muskrat), Stockard and Papanicolaou, 1919 (guineapig), Marshall, 1904 (ferret), and Wright, 1931 (skunk). Both sexes are fully aware of these conditions; their reciprocal behavior reflects this knowledge. It is not impossible that exceptions to the rule of female control may sometime be discovered among mammals other than man. But, if they occur at all, such exceptions seem likely to be so uncommon as to have little

or no influence on the formation of species habits. In man the conditions are radically different. Here the males possess the ability to take sexual advantage of their superior physical strength, and this circumstance appears to have made an indelible impression on the thinking and acting of the species as a whole.

The influence of these four "normal" elements of human behavior can be traced in the social systems of all peoples. This is inevitable because an important part of every such system is the experimental handling of a problem in which those elements play a very important part. Man is a gregarious, property recognizing primate whose sexual behavior is not subject to great seasonal or other fluctuation, whose young pass through an exaggerated phase of the long period of dependence on the parents common to most primates, whose adults possess the incompatible tendencies to form long continuing sexual partnerships and to become sexually indifferent or antagonistic through exclusive association, and, finally, whose males have the very unusual power to force their sexual will on the females. When he began to live in groups more intricate in structure and more dense in population than those that met the needs of other primates man found that these natural characteristics did not lead to harmonious sexual adjustment. They had to be checked and modified by cultural controls. How, then, should the required checks be applied? In their marriage customs the existing tribes and peoples have brought forward countless attempted solutions of this baffling and perhaps insolvable problem, as may be seen particularly well recorded in such works as Westermarck's *History of Human Marriage*, Margold's *Sex Freedom and Social Control*, and Briffault's *The Mothers*.

No one doubts that the conflict between

man's strong inclination to form sexual partnerships and his primate tendency to tire of his mate is one of the disturbing elements in every social system. It has supplied the material for much of the world's literature and drama. Nothing further will be said about it here. But the cultural importance of the facts that human sexual behavior is in accord with mammalian type No. 3 and that in man alone among mammals the ability to make the final sexual decision has passed from the female to the male needs a few more words.

MAN'S SEXUAL BEHAVIOR TYPE AND THE PROBLEM OF PROMISCUITY

Among the many controversial details pertaining to our ideas about human social beginnings one of the most discussed is the question whether or not the existing forms of marriage have been developed from an earlier system or condition of sexual promiscuity. On this subject the most diverse and contradictory opinions are to be found in the writings of experienced authorities. For instance, Bloch declared (1908, p. 188) that

Since the subject first engaged my close attention, it has always seemed to me incomprehensible that a dispute should ever have arisen among anthropologists, ethnologists, and historians of civilization as to whether, among the primitive forms of the sexual relationship, marriage was the first, or whether it was preceded by a state of sexual promiscuity. Whoever knows the nature of the sexual impulse, whoever has arrived at a clear understanding regarding the course of human evolution, and, finally, whoever has studied the conditions that even now prevail, alike among primitive peoples and among modern civilized races, in the matter of sexual relations, can have no doubt whatever that in the beginnings of human development a state of sexual promiscuity did actually prevail.

Westermarck, on the contrary, devotes no less than 234 pages of the revised edition of his *History of Human Marriage*

(1922) to a criticism of the hypothesis of promiscuity. His attitude may be learned from the following quotations (vol. 1, pp. 103, 336):

It is often said that the human race must have originally lived in a state of [sexual] promiscuity. . . . This opinion has been expressed by Bachofen, McLennan, Morgan, Lord Avebury, Giraud-Teulon, Lippert, Kohler, Post, Wilken, Kropotkin, Wilutzky, Bloch, and many others. . . . It is not, of course, impossible that among some peoples the intercourse between the sexes may have been almost promiscuous. But the hypothesis according to which promiscuity has formed a general stage in the social history of mankind . . . is in my opinion one of the most unscientific ever set forth within the whole domain of sociological speculation.

More recently Briffault (1927, vol. 2, pp. 1-96) has severely criticized Westermarck's handling of data. He concludes that marriage is an economic relation not originally associated with claims of exclusive sexual possession, and that freedom as regards extra-marital sexual relations is wide-spread and subject to little or no opprobrium in most societies. Economic considerations may in rare cases set a price on virginity; but the facts derived from a survey of all the cultures with which we are acquainted do not warrant the assumption that a regard for prenuptial chastity is widely held. Furthermore, he writes (1927, vol. 2, pp. 95, 96; 1931, p. 69):

Individual marriage is, in its origin, not rooted in any form of association between sexual partners, or in any group, or family, resulting from such association, but is, even in its most primitive and rudimentary forms, distinguished as a juridic relation, irrespectively of its stability or of any group or family which may or may not be formed from sexual relations that are not thus juridically established. . . . Very commonly, and in quite primitive societies, the juridic relation is not established until relatively late in life, on the ground of purely economic considerations; but sexual relations not so established, that is to say, pre-nuptial relations, are not in any way regarded as irregular or derogatory.

Whether it be supposed that the earliest human social aggregates were formed by the multiplication

and continued association of single pairs, or by the aggregation of several groups, comes to the same thing. According to every biological precedent the larger group must, in the absence of evidence to the contrary, be assumed to have been entirely promiscuous as regards sex relations. The problem of social origins is that of accounting for the introduction of sexual restrictions and regulations in such a promiscuous group.

After reviewing what is actually known of social grouping in non-human primates Zuckerman concludes (1929, pp. 83, 88):

The harem is the social unit of monkeys and apes, and one may recognise two main types of society arising from it. The first, exemplified by the societies of the majority of tree monkeys, consists of the single harem living alone. The second is the society formed by the union of several harems. The best examples of this type are the societies of baboons, who are very seldom reported in troops of less than twenty, and have been seen in hordes consisting of as many as three hundred individuals. An intermediate type also occurs, several harems uniting to form temporary associations.

It was from a similar social level, so far as one can tell, that, in the Oligocene or Miocene, an anthropoid set out on its journey towards manhood. Nothing is known about this journey. At the one extreme there is the anthropoid in its harem, a frugivorous animal who reveals just the beginnings of a reasoning process. At the other is man, whose every activity is culturally conditioned. The only possible social sphere of comparison between the two is the family, yet nowhere in the human world does one see anything approaching the harem of the infrahuman Primate. One fact is, however, clear. There is no need to search for cultural factors to account for man's permanent sexual association [i.e. permanent association in groups consisting of both males and females], for this feature is one shared by all Primates alike.

These opinions are representative of the many that have been expressed. Part of the conflict among them seems to arise from the circumstance that many writers not only human but also primate, and that leave out of account the fact that man is some lines of cultural development may therefore have had their beginnings among ancestral creatures that were not the same as the men of today. Lowie, for instance,

declares, in discussing the question of early promiscuity (1930): "Nevertheless, it holds true that *on the human level* (italics his) the individual family is never abrogated by such usages [sexual licence]. I, for one, am dealing with Andamanese, Australians, Chukchi, not with *Homo alalus*, or *Pithecanthropus*." To writers who thus limit their attention to conditions existing in living races the discovery that some trace of social control of the mutual relations of the sexes can everywhere be found today proves that man has always exercised such control. This conclusion, however, neglects the very important circumstance that no living race of man is primitive in the zoological sense. But the fact cannot be too strongly insisted upon that all present day races, whether considered as primates or as members of the family *Hominidae*, are highly specialized physically—for instance, in their gigantism and in the advanced adjustment of their skull, pelvis, and foot to the upright posture—and that this specialization points to the former existence of many long series of extinct races with which we are not now acquainted. Hence the search among these specialized existing peoples for a race or tribe living under social conditions that represent anything closely resembling an unmodified reflection of man's primitive mentality can have little chance of success. Another significant fact that has not been given its due weight in these discussions is the obvious circumstance that the principal checks imposed by every group on the sexual conduct of its members are checks on promiscuity, that is to say, checks imposed, for the benefit of some cultural scheme, on mammalian behavior of type No. 3.

A final source of confusion lies in the ambiguousness of the term *promiscuous* as it is commonly used. It is quite possible that few mammals are promiscuous in the

extreme sense of breeding without any trace of individual choice on the part of either the male or the female. If this definition be insisted on the term necessarily becomes meaningless as applied to man and other primates. Nevertheless it appears to have been the one used by Zuckerman (1930, p. 725) when he wrote: "Moreover, monkeys are not promiscuous. The literature provides sufficient evidence to enable one to make the generalization that the tendency of sub-human male primates is toward polygyny. Every adult male attempts to secure for himself as many females as possible. There is no selection." On the other hand, promiscuity in the sense of the habitual formation of temporary, fluctuating, sexual associations is a term applicable to much of the recently observed primate behavior. This appears to be the usually accepted meaning of the word. It is the one that I here adopt.

It would be difficult to imagine a more convincing picture of a mammal fundamentally promiscuous, as the word has just been defined, than the one painted by Westermarck in the six chapters of his criticism of the hypothesis of human promiscuity. Only, instead of approaching his subject directly, after the manner of Kempf or Hamilton, he approaches it indirectly by outlining the multitudinous devices adopted by different social units in their attempts to modify a kind of behavior perfectly suited to the needs of primates roaming the forest in relatively small, simply constituted bands, so as to make it fit the needs of primates that have developed more sedentary, larger, and more complicated social groups.

EVIDENCE OF PROMISCUITY FURNISHED BY OUR OWN SOCIETY

Furthermore, when we examine the society that we know best, namely, our

own, we find abundant evidence that a considerable part of the sexual activity of its members is regulated even today by the rules of promiscuity that grow out of behavior type No. 3.

As long ago as 1904 Frey wrote (as quoted by Bloch, 1908, p. 190):

Ports in which ocean-going vessels come to harbor are familiar with the sexual impulse in its most completely animal form. . . . We find ourselves transported into the depths of an urgent primitiveness . . . and this will enable us to form an idea of the bestial indifference in sexual matters that must have obtained amongst the herds of primitive man.

But it is not necessary to visit sailor's resorts in order to obtain evidence that this "urgent primitiveness," or, in other words, behavior type No. 3, is constantly at work. The annals of prostitution illustrate it perfectly. Prostitution is often studied as a strictly economic phenomenon. And, undoubtedly, many women are driven to it by poverty. But the fact is generally overlooked that this form of activity could not offer the slightest relief from economic pressure to any mammal that might be psychologically monogamous, or to one whose sexual behavior was not of the type No. 3, that is to say, it would be economically valueless except to one whose female was always both attractive and receptive and whose male was always producing sperm. How true this is will be realized if we reflect on the economic worthlessness that prostitution would possess if the human breeding instinct were active, as it is in some mammals, during a single yearly period of a few weeks only; or if the sexual attractiveness of the human female to the male were limited, as it is in many other mammals, to a few days in each month. The conduct of the prostitute and her patrons seems, therefore, most reasonably interpreted if it is regarded, not as a social phenomenon generated by the forces of special-

ized civilizations, but as the commercialized survival of a promiscuous condition through which every human society has probably been forced to pass, by virtue of man's primate sexual behavior type.

While no adequate statistics can be found in print there is little cause to doubt that prostitution in European society and its derivatives, is both abundant and widely spread. Prostitution therefore cannot do otherwise than furnish to the many members of that society, both male and female, who desire it, for one reason or another, the opportunity to live a sexual life—temporarily or permanently—that conforms with a common primate type of behavior. The ease with which this mode of life is adopted has puzzled many moralists. It is not hard to understand when viewed by comparative psychology's light.

Another good indicator of the wide extent to which promiscuous behavior prevails in our society is furnished by the history, both past and present, of the venereal diseases. Buret has given (1895) an account of the epidemic of syphilis that swept through Europe at the end of the fifteenth century. The rapidity with which the disease spread is clear evidence of the sexual promiscuity that existed in the European society of four hundred years ago.

Coming down to the present day we find that there are differences of opinion as to the incidence of the venereal diseases in the general population.

Cabot (1916, pp. 365, 366) found that 33 per cent of the men over 16 years of age examined in the medical wards of the Massachusetts General Hospital (Boston) were aware that they had had gonorrhea. Syphilis was less prevalent in their recollections; nevertheless "about 25 per cent of hospital patients show a positive Wassermann reaction." During our partici-

pation in the world war Levin (1919) calculated, on the basis of more than 10,000 blood tests administered to newly enlisted soldiers gathered from all walks of life, that the proportion of syphilitics was about 16 per cent among the white men and about 36 per cent among the colored. Stanley (1929) has reported that 15 per cent of 10,000 male prisoners examined in the California State prison gave a history of venereal sore. The positive Wassermann reactions were as follows: white men (8,004), 7.2 per cent; negroes (530), 18.1 per cent; Mexicans (1,265), 15.6 per cent. Wassermann tests given to 1976 patients (sex not stated) in the Moses Taylor Hospital, Scranton, Pa., showed a positive percentage of only 6.3, as communicated to me by Dr. J. M. Wainwright. Concerning gonorrhea, Dr. J. Allen Gilbert, assistant professor of medicine in the University of Oregon, and medical adviser, Oregon Board of Health, declares (1916, p. 53) that we are perfectly safe in saying that from 70 to 75 per cent of all adult men have had the disease at some time in their life. Among the California prisoners Stanley (1929) found that 48.2 per cent "gave a history of gonorrhea which cannot well be mistaken." Blashko and Erb (as quoted by Bloch, 1908, p. 394) independently found, in Germany, that of the men who entered on marriage for the first time when above the age of thirty years, each one had, on the average, had gonorrhea twice, and about one in four or five had been infected with syphilis. Whichever figures or estimates are taken as most nearly representing the truth it cannot be doubted that they give unmistakable evidence of wide spread behavior in perfect conformity with type No. 3.

There is thus abundant proof that the tendency to behave promiscuously exists in our own society; and the same is true of every society with which we are ac-

quainted. It is equally clear that all marriage systems are largely devices to check and regulate promiscuous behavior in the interest of human economic schemes. When we consider how universally the need of these devices is recognized, and how imperfectly they function after countless generations of trial, it seems hard to doubt that general promiscuity, conforming with behavior type No. 3, has been an experience, at some period of its evolution, of the genus to which man belongs. This racial experience, no matter when it was passed through, seems to have transmitted such a deep impression to modern mankind that it must be counted as one of the important factors that have helped to shape the social systems of today.

THE SOCIAL INFLUENCE OF RAPE

The fact that human male force can in the end be sexually effective is accepted without dispute. Doubts may arise with regard to special stories; but no one questions the essentially true nature of traditions like the Rape of the Sabines, or of old chronicles like the rape of Tamar by her half brother Amnon (2 *Samuel*, 13: 1-15) and the death of the Levite's concubine on the morning after the men of Gibeah had subjected her to a night of multiple rape (*Judges*, 19: 24-30). Still less is general skepticism aroused by newspaper accounts of the latest assault case with its subsequent lynching. But, though the reality of this kind of behavior is admitted, the considerable part that rape may well have taken in shaping human customs seems not to have received all the attention that is its due.

I have already (p. 395) tried to show how specifically human is the transfer of the final decision in sexual intercourse from the female to the male. This transfer, much though it might be welcomed by the males of other animals that are subject

to continuous spermatogenesis, appears to have become a racial characteristic of man alone among mammals because of man's high mental development combined with his extreme pelvic adaptation to the upright posture. I now wish to speak of some cultural results of this transfer. As an introduction I shall quote from Briffault (1927, vol. 2, pp. 21-22). The passage is particularly interesting because it shows how widely distributed rape is outside of our own society, and also because it indicates the manner in which social behavior begins to be influenced by this peculiar feature of human sex ways.

The dangers of such violence are in primitive societies very real. In Australia any female found unprotected is invariably abused and often killed afterwards. In East Africa, among the Wayao and other tribes, a man, we are told, will never pass a solitary unmarried girl without entering into sexual relations with her, and if she refused he would probably kill her. So likewise among the Andaman Islanders an unmarried girl who repels a man runs the risk of being killed. Among the Siouan tribes of North America, "a man has as little control over his passions as any wild beast, and he is held as little accountable for their indiscriminate gratification." Rape was extremely common. Among the Pima Indians the young men actually used lassoes to catch any stray female they might find. Hence among the plain tribes, "custom makes it not only improper, but very dangerous for an Indian woman to be found alone away from her lodge; for an unmarried girl to be found away from her lodge alone is to invite outrage, consequently she is never sent out to cut and bring wood, nor to take care of stock." Further, it was the practice among all those tribes for unmarried girls when they went out at night to meet a lover, or to some 'dance,' to tie a rope round their thighs in such a manner that, while it did not interfere with their movements, it served as an effective preventive against violence on the part of the men.

The different types of social behavior that appear to have had their exact form influenced by masculine control of the sexual decision are chiefly of two kinds: those that resist or avoid this control and those that make use of it.

Among the customs that resist or avoid this feature of male dominance we find conventions, like those mentioned by Briffault, in which social proprieties, restrictions of feminine economic activities, and details of feminine dress, owe their origin to fear of male aggression. A careful search for customs of this kind would probably show that they are many and widely spread. Our own society is not without its social usages that seem to reflect the same fears that once beset the plains Indian squaws. Unaccompanied women, for instance, do not avoid certain districts of our cities after nightfall simply because of a supposed or real danger of robbery. The threat of sexual violence is always present in the background of this taboo as well as in the social criticism that infraction of the rule so often elicits. The peculiar behavior patterns so much talked about and written about as "animosities between the sexes" and as "feminine guiles" should also be considered. These may well have arisen, in part at least, from the common primate tendency to use sexual ruses for self protection, stimulated to specialized developments by the biologically unusual sexual dominance of the human male. It would seem highly improbable that they could ever have assumed any social importance if women, like female monkeys, possessed unquestioned sexual control of their persons by virtue of physical fact, and consequently were not subjected to an ever present conflict between the accepted fiction that they are free to choose and the never entirely forgotten reality that in the last appeal they are not.

Other social features of the same type may be detected in the strongly emotional reaction to rape in our society. As illustrations we have only to think of the frequency with which this emotion is exploited in literature, on the stage and on

the screen, and also to remember the excessive severity of legal repressive measures, and the flourishing condition of blackmail, as recently described by Robinson (1929, pp. 307-315). Throughout the southern United States the same emotion complicates the problem of social adjustment between negroes and whites; and it was appealed to for purposes of propaganda during the world war.

Passing now to the social conventions that turn male sexual dominance to account we find the many marriage customs in which the preference of the woman is slightly or not at all considered,—a long catalogue of practices that includes on the one hand such realistic items as marriage by capture or purchase, the exchanging or lending of wives, and on the other hand such now empty formalities as our own ceremony of giving away the bride by her father or by some other male relative. The pawning of women as practiced in Liberia is a frankly commercialized specialization (Strong, 1930, vol. 1, p. 70, fig. 48). Briffault (1927, vol. 3, pp. 404-405) has shown how, in Europe during the age of chivalry, the rape of an unaccompanied woman was socially condemned, whereas rape after the fair conquest of a woman's male escort was regarded with complacency. The institution of child marriage, particularly as we find it in Australia and India, with its sanctioned physical injury of small girls by adult men (See Briffault, 1927, vol. 2, p. 60; Indian Legislative Debates of 1922, vol. 3, pt. 1, appendix, p. 919; Mayo, 1931, also 1927, pp. 11-62; *Journ. Amer. Med. Assoc.*, vol. 95, p. 1188, October 16, 1930) is another social exploitation of this prerogative of the human male, coupled, however, with a somewhat unusual specialization of the primate tendency—one of the features of oestrus-free behavior—for adults to take sexual interest in individuals of prepubertal age.

In India this last peculiar item of man's primate heritage is definitely turned to social account, while in European civilization it is outlawed. Trevor Pinch, formerly editor of *The Civil and Military Gazette*, India, writes of it (1930, p. 116):

Primarily arising from the sex-obsessions which I have already described, it is enjoined upon men, youths, and even mere boys, that they should mate with young and virgin girls. Many observers have placed it on record that this marked preference for girl-children of very tender age is a disturbing and discreditable feature of Hindu life. Still, the fact must be faced. He who would shut his eyes to it is a fool.

In France the criminal statistics covering a period of 25 years showed that there were 17,657 convictions for sexual assault on girls less than 16 years of age, while, during the same period there were only 4,360 convictions for assault on adult women (Tardieu, 1878, pp. 18-19). Exactly how much of this discrepancy arose from the better means of defense available to grown persons as compared with children is not certain; but the figures strongly suggest the existence in European men of a type of impulse closely similar to the one that moves the adult Hindu when he seeks a child wife and legally maims her.

Those types of human polygamy in which the wives are obtained through transactions between men and are afterwards held in virtual servitude may also owe their original establishment and their exact present form in some part to the specifically human male sexual dominance. In any event, such associations fundamentally differ from the polygamous groupings with which we are acquainted in other mammals, particularly in seals and ungulates. The social function of the male horse, deer, or fur seal, so far as reproduction is concerned, doubtless includes some "herding" of the females, as well as some fighting off of masculine rivals. But, in these non-human sexual groupings, it is obviously the general rule that the

females at their own appropriate physiological season voluntarily accept and associate with the male and as voluntarily refuse and desert him when impregnation has been accomplished. Therefore non-primate polygamy and the human types of polygamy in question, though they may superficially resemble each other, actually rest on unlike psychological bases; and the distinguishing characteristics of each system are exactly those that might be expected to have arisen under the contrasting influences of control of the sexual decision by the female in seals and ungulates and by the male in man. The following descriptions of two polygamous groups should make this distinction clear.

In the Alaskan furseal, one of the most extremely polygamous of mammals, the males, as we have already seen (p. 382), are the first to arrive at the breeding grounds. Because each bull must remain at his post to defend it against rivals there is no seeking and capturing of mates. When the females come to land they go of their own accord to the males, and the most that any bull can do is to seize with his teeth some cow that passes within reach. From ten to forty-eight hours after the birth of her young each female solicits reimpregnation. Concerning the female's behavior at this time and the male's subsequent attitude toward her Elliott (1884, pp. 110-111) is very definite. He says:

The cow always makes the first advances to the bull. If she is one of the earlier subjects for his attention, the union is soon accomplished; but should she be of the later applicants in his harem, after he has been more or less exhausted by the vital drafts made upon him, she must wait. I have observed instances of this character in which the female teased the male for hours and hours before arousing him. . . . She is satisfied [after one act of copulation], and passes rapidly out of heat. Certain it is that she is not noticed by him again; she goes up to his seraglio-grounds, to and from the sea, seeking her young and feeding undisturbed for the balance of the time; also,

that the other bulls seem to recognize this condition of passed sexual requirement and satisfaction, in her case, by paying her no attention.

Perhaps the baboon harems studied by Zuckerman may present a nearer approach to human conditions than is seen in the foregoing example of animal polygamy; but the details, unfortunately, are not available at the time of going to press.

The strikingly different character of a human polygamous association is well brought out by Post Commander G. Reynaud's account (1911, pp. 870-871) of a wealthy Moroccan's harem.

Ahmed passes for a very virtuous man because every year he joins the pilgrimage to Mecca. On arriving in Asia Minor he interrupts his pious journey to go to Constantinople and especially to Bursa, whence he brings home pretty Circassian girls purchased at a high price. He has thus built up an enchanting collection of beautiful women, which I once had the opportunity to admire. Invited to lunch at his home I was received by my host at the doorway. Three widely spaced strokes of a knocker announced to the feminine members of the household that it was time for them to disappear. The women were given the time necessary to eclipse themselves: all remained crowded in dense ranks in the colonnade-surrounded courtyard, and, after having allowed themselves to be seen, they ran riotously away. . . . Many people think that Musulman women accept polygamy without objection. . . . And indeed, when all dignity is debased in these unfortunate creatures on whose soul and body forcible hands have been laid, they accept with resignation the inevitable, and murmur the word of the fatalist: "*Mektoub*,"—*it was written*.

The custom of *purdah*, or strict cloistering of women, as it now exists in India, seems to rest, in some part, at least, on both the exploitation and the fear of male aggression. In describing it Katherine Mayo writes (1927, pp. 112-113):

That view of women which makes them the proper loot of war was probably the origin of the custom of *purdah*. When a man has his women shut up within his own four walls, he can guard the door. Taking Indian evidence on the question, it appears that in

some degree the same necessity exists today. In a part of India where *purdah* but little obtains, I observed the united request of several Hindu ladies of high position that the Amusement Club for English and Indian ladies to which they belong reduce the minimum age required for membership to twelve or, better, to eleven years. This, they frankly said, was because they were afraid to leave their daughters of that age at home, even for one afternoon, without a mother's eye and accessible to the men of the family.

Far down the social scale the same anxiety is found. The Hindu peasant villager's wife will not leave her girl child at home alone for the space of an hour, being practically sure that, if she does so, the child will be ruined. I dare not affirm that this condition everywhere obtains. But I can affirm that it was brought to my attention by Indians and by Occidentals, as regulating daily life in widely separated sections of the country.

It seems difficult if not impossible to explain the origin and maintenance of social behavior patterns such as these except on the ground that, whatever strictly economic elements they may contain, they all owe important features of their exact form to the knowledge possessed by both sexes that the physical control of the sexual decision belongs, in last resort, not to the females but to the males.

SUMMARY AND CONCLUSION

The main characteristics of human sexual behavior, contrary to a widely prevalent belief, are not peculiar to man. Though they differ conspicuously from the characteristics of sexual behavior displayed by domestic ungulates and carnivores, most of them are shared by man with several non-human primates that have been subjected to comparative psychological study. In this department of his behavior man has invented nothing essentially new; the relatively unimportant human behavior patterns that have not been identified in other members of the order Primates can probably all be explained as specializations of behavior that

is known to occur among non-human Old World members of the group.

Only two of these human specializations are of such a nature that they appear to have had any significance in directing the general course of cultural development. The first is that man seems to have a stronger tendency than most other primates to form continuing sexual partnerships. The second is that in man alone of all mammals is the male known to be able to force his sexual will on an unconsenting or unconscious female, a peculiarity that seems to arise from human ingenuity combined with the human pelvic adjustments to the upright posture.

These two special human features, together with two others that belong to the general primate heritage, namely, the freeing of the sexual instinct from the sharply defined physiological rhythms that direct it in other mammals, and the often rapid "fatigue of the sexual sensorimotor system through excessive stimulation by a too constant object" provide human society with some notably discordant behavioral elements. Unreasoned attempts to control these elements in the interest of varying cultural trends seem to have been the principal sources of the multitudinous systems of marriage that exist in the world today.

The fact that man's sexual behavior is not governed by sharply defined physiological rhythms gives powerful support to the view that the human societies now in existence have developed from an earlier condition of sexual promiscuity consistent with this free type of behavior. The circumstance that no societies now exist without some kind of formal marriage has little bearing on the question, because all living members of the genus *Homo* are highly specialized in the zoological sense, and all present-day societies, not excepting the less efficient ones that are usually but

misleadingly called "primitive," must therefore owe the cultural features that now distinguish them from one another to an extremely long process of evolution. That sexual promiscuity—in the sense of an habitually temporary and fluctuating association of sexual partners—is a phase ancestral to the existing social systems is further indicated by the facts (a) that marriage customs, taboos, and laws are largely attempts at curbing just such promiscuity, and (b) that both premarital and extramarital promiscuity can easily be shown to flourish in most societies, including our own.

The passing of the control of the sexual decision from the female to the male is a human peculiarity that has probably influenced many lines of social development. Some customs, such as particular standards of feminine social propriety and many

restrictions of feminine activities, reflect the fear of male aggression. Others, such as those marriage customs that largely eliminate feminine preference, also child marriage by adult men, and the more specialized forms of human polygamy turn this aggressive ability to direct account.

The sexual psychology of man together with the social usages whose forms have been influenced by it can never be fully understood through the study of man alone any more than human anatomy and physiology can be so understood. It is on comparative studies that sound results must depend.

This paper was originally prepared as a contribution to the "Second International Congress for Sex-Research," which convened in London, August 3-9, 1930. Because of its length it was read by title only. Returned to the author it has been revised to date of August, 1931.

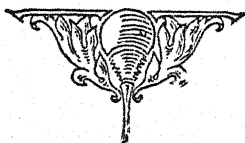
LIST OF LITERATURE


- [ANON.] 1922. Indian Legislative Debates of 1922, vol. 3, pt. 1, appendix.
- [ANON.] 1930. Journ. Amer. Med. Assoc., vol. 95, p. 1188. October 16, 1930.
- BAKER, 1930. The breeding season in British wild mice. Proc. Zool. Soc. London, 1930, pt. 1, pp. 113-126, pl. 1.
- BASEDOW, 1927. Subincision and kindred rites of the Australian aboriginal. Journ. Royal Anthropol. Inst. Gr. Brit. and Ireland, vol. 57, pp. 123-156. June, 1927.
- BINGHAM, 1928. Sex development in apes. Comparative Psych. Monographs, Baltimore, vol. 5, no. 1, pp. 1-165. May, 1928.
- BLANFORD, 1888-1891. Fauna of British India, Mammalia. Taylor and Francis, London.
- BLOCH, 1908. The Sexual Life of our Time, translated by M. Eden Paul. Allied Book Co., New York.
- BRANDES, 1930. Die Begattung des Orangs. Zool. Garten, Leipzig, n. F., vol. 3, pp. 216-217.
- BRIFFAULT, 1927. The Mothers: a Study of the Origins of Sentiments and Institutions. 3 vols. Macmillan Co., New York.
- , 1931. The Mothers: the Matriarchal Theory of Social Origins. 1 vol. Macmillan Co., New York.
- BURET, 1895. Syphilis in the Middle Ages and in Modern Times (translated by A. H. Ohman-Dumesnil). Davis Co., Philadelphia.
- CABOT, 1916. A Layman's Handbook of Medicine. Houghton, Mifflin Co., Boston and New York.
- CATON, 1881. Antelope and Deer of America. Houghton, Mifflin Co., Cambridge, U. S. A.
- COURRIER, 1927. Étude sur le déterminisme des caractères sexuels secondaires chez quelques mammifères à activité testiculaire périodique. Arch. Biol. (Van Beneden), Liège—Paris, vol. 37, pp. 173-334.
- CREW and MISKATA, 1930. Mating during pregnancy in the mouse. Nature, vol. 125, p. 564. April 12, 1930.
- DAVIS, 1926. Periodicity of sex desire, Part 1. Unmarried women, college graduates. Amer. Journ. Obstetr. and Gynecol., vol. 12, pp. 824-838. December, 1926.
- ELLIOTT, 1884. The Habits of the Fur-Seal. The Fisheries and Fishery Industries of the United States, Section 1, Natural History of useful Aquatic Animals, Part 1, Mammals, pp. 75-113.
- ELLIS, 1904. Analysis of the Sexual Impulse. Davis Co., Philadelphia.
- , 1928. Studies in the Psychology of Sex, vol. 7. Davis Co., Philadelphia.

- EIPPER, 1929. *Animals Looking at You* (translated by Patrick Kirkwan). Viking Press, New York.
- FOX, 1929. The birth of two anthropoid apes. *Journ. Mamm.*, vol. 10, pp. 37-51. February 11, 1929.
- GEAR, 1926. The oestrous cycle of the baboon. *South African Journ. Sci.*, vol. 23, pp. 706-712. December, 1926.
- GILBERT, 1916. True and False Sex Alarms. Reberman, New York.
- HAMILTON, 1914. Sexual tendencies of monkeys and baboons. *Journ. Anim. Behavior*, vol. 4, pp. 295-318. October, 1914.
- 1925. *An Introduction to Objective Psychopathology*. C. V. Mosby Co., St. Louis.
- 1929. *A Research in Marriage*. Albert and Charles Boni, New York.
- HARTMAN, 1928. The period of gestation in the monkey, *Macacus rhesus*, first description of parturition in monkeys, size and behavior of the young. *Journ. Mamm.*, vol. 9, pp. 181-194. August 9, 1928.
- 1931. The breeding season in monkeys, with special reference to *Pithecus* (*Macacus*) *rhesus*. *Journ. Mamm.*, vol. 12, pp. 129-142. May, 1931.
- HEAPE, 1900. The "sexual season" of Mammals and the relation of "pro-oestrus" to menstruation. *Quart. Journ. Microscop. Sci.*, London, vol. 44, pp. 1-70.
- 1905. Ovulation and degeneration of ova in the rabbit. *Proc. Roy. Soc. London, B*, vol. 76, pp. 260-268.
- KEMPF, 1917. The social and sexual behavior of the infra-human primates with some comparable facts in human behavior. *Psychoanalytic Review*, Washington, vol. 4, pp. 127-154. April, 1917.
- KIERNAN, 1917. Kleptolagny or kleptomania. *Urologic Review*, St. Louis, vol. 21, pp. 43-45. January, 1917.
- KÖHLER, 1925. *The Mentality of Apes*. Translated by Ella Winter from the second revised German edition. Harcourt, Brace & Co., New York.
- LATASTE, 1886-1889. Documents pour l'Éthologie des Mammifères. *Actes Soc. Linn. Bordeaux*, vol. 40, pp. 292-466, 1886; vol. 41, pp. 201-536, 1887; vol. 43, pp. 61-208, 1889.
- LEVIN, 1919. The incidence of syphilis among white and colored troops as indicated by an analytical study of the Wassermann results in over ten thousand tests. *Journ. Lab. and Clin. Med.*, St. Louis, vol. 5, pp. 93-106. November, 1919.
- LONG and EVANS, 1922. The oestrous cycle of the rat and its associated phenomena. *Mem. Univ. California*, vol. 6, pp. 1-148. June 28, 1922.
- LOUTTIT, 1927. Reproductive behavior of the guinea pig. 1. The normal mating behavior. *Journ. Comp. Psych.*, vol. 7, pp. 251-257. June, 1927.
- LOWIE, 1930. [Review of Miller, 1928.] *Amer. Anthropol.*, n.s., vol. 32, p. 168. January, 1930.
- LUCAS, HUME, and SMITH, 1927. On the breeding of the common Marmoset (*Hapale jacchus* Linn.) in captivity when irradiated with ultra-violet rays. *Proc. Zool. Soc. London*, pp. 447-451. April, 1927.
- MACKINTOSH and WHEELER, 1929. Southern Blue and Fin Whales. *Discovery Reports*, vol. 1, pp. 257-540. University Press, Cambridge, England.
- MALINOWSKI, 1927. *Sex and Repression in Savage Society*. Harcourt, Brace & Co., New York.
- 1929. *Sexual Life of Savages in Northwestern Melanesia*. 2 vols. Horace Liveright, New York.
- MARGOLD, 1926. *Sex Freedom and Social Control*. University of Chicago Press. November, 1926.
- MARSHALL, 1904. The oestrous cycle of the common ferret. *Quart. Journ. Microscop. Sci.*, n.s., vol. 48, pp. 323-345. September, 1904.
- MATTHEWS, 1929. The natural history of the elephant seal with notes on other seals found at South Georgia. *Discovery Reports*, vol. 1, pp. 233-256. University Press, Cambridge, England.
- MAYO, 1927. *Mother India*. Harcourt, Brace & Co., New York.
- 1931. *Volume Two*. Harcourt, Brace & Co., New York.
- McDOUGALL, 1923. *Outline of Psychology*. Charles Scribner's Sons, New York.
- 1926. *Outline of Abnormal Psychology*. Charles Scribner's Sons, New York.
- MIDDLETON, 1931. A contribution to the biology of the Common shrew, *Sorex araneus* Linnaeus. *Proc. Zool. Soc. London*. pt. 1, pp. 133-143. April, 1931.
- MILLER, 1928. Some elements of sexual behavior in primates and their possible influence on the beginnings of human social development. *Journ. Mamm.*, vol. 9, pp. 273-292. November 13, 1928.
- MOLL, 1912. *Handbuch der Sexualwissenschaften*. F. C. W. Vogel, Leipzig.
- MONTANÉ, 1915. Notas sobre un chimpancé nacido en Cuba. *Mem. Soc. Cubana Hist. Nat.* "Felipe Poey," vol. 1, pp. 259-269. Separates issued, repaged 1-17 (without reference to the original publication) under the title, *Un chimpancé Cubano*, "El Siglo XX" publishing company, Havana, 1915. Translation by X. A. Prossy,

- Journ. Anim. Behavior, vol. 6, pp. 330-333. August, 1916.
- MONTANÉ, 1928. Histoire d'une famille de chimpanzés. Étude physiologique. Bull. et Mém. Soc. Anthropol. Paris, 1928, pp. 14-35. Separates issued, repaged 1-21 (without indication of the original place of publication).
- NELSON, 1929. Oestrus during pregnancy. Science, n.s., vol. 70, pp. 453-454. November 8, 1929.
- PASSEMARD, 1927. Quelques observations sur des chimpanzés. Journ. Psych. Norm. et Path., vol. 24, pp. 243-253. March 15, 1927.
- PINCH, 1930. Stark India. Hutchinson & Co., London.
- RETIÉ DE LA BRETONNE, 1883. Monsieur Nicolas. 14 vols. Isidore Liseux, Paris.
- REYNAUD, 1911. Notes sur la vie marocaine. Revue des Deux Mondes, year 81, vol. 6, pp. 870-871. December 15, 1911.
- ROBINSON, 1929. America's Sex Marriage and Divorce Problems. Eugenics Publishing Co., New York.
- ROOSEVELT, 1910. African Game Trails. Charles Scribner's Sons, New York.
- ROOSEVELT and HELLER, 1914. African Game Animals. 2 vols. Charles Scribner's Sons, New York.
- ROUSSEAU, 1914. Confessions. Van Bever Ed. 3 vols. Georges Crès et Cie, Paris.
- SCHUSTER, 1929. Ein Beitrag zur Frage der Brunst- und Setzzeiten der Säugetiere in den Tropen. Zool. Garten, Leipzig, n. F., vol. 2, pp. 114-117. October, 1929.
- SETON, 1909. Life-histories of North American Animals. 2 vols. Charles Scribner's Sons, New York.
- 1925-1928. Lives of Game Animals. 4 vols. Doubleday Page & Co., New York.
- SOKOLOWSKY, 1923. The sexual life of the anthropoid apes. Urologic and Cutaneous Review, vol. 27, pp. 612-615. October, 1923.
- SLADE, 1903. On the mode of copulation of the Indian elephant. Proc. Zool. Soc. London, 1903, vol. 1, pp. 112-113.
- STANLEY, 1929. Syphilis among state prisoners. Journ. Amer. Med. Assoc., vol. 92, p. 1138. April 13, 1929.
- STOCKARD, 1930. Observations on the seasonal activities of the white-tailed prairie-dog *Cynomys leucurus*. Papers Michigan Acad. Sci. Arts and Letters, vol. 11, pp. 471-479.
- STOCKARD and PAPANICOLAOU, 1919. The vaginal closure membrane, copulation, and the vaginal plug in the guinea-pig, with further consideration of the oestrous rhythm. Biol. Bull., vol. 37, pp. 222-245. July, 1919.
- STRONG (and associates), 1930. The African Republic of Liberia and the Belgian Congo. 2 vols. Harvard University Press, Cambridge, U. S. A.
- SVIHLA, 1930. Breeding habits and young of the red-backed mouse (*Evotomys*). Papers Michigan Acad. Sci. Arts and Letters, vol. 11, pp. 485-490.
- 1931. Life history of the Texas rice rat (*Oryzomys palustris texensis*). Journ. Mamm., vol. 12, pp. 238-242. August, 1931.
- SVIHLA and SVIHLA, 1931. The Louisiana muskrat. Journ. Mamm., vol. 12, pp. 12-28. February, 1931.
- TARDIEU, 1878. Étude Médico-Légale sur les attentats aux mœurs, 7th ed. Baillière, Paris.
- THOMAS, 1909. Source Book for Social Origins. Univ. of Chicago Press.
- TINKLEPAUGH, 1928. The self-mutilation of a male *Macacus rhesus* monkey. Journ. Mamm., vol. 9, pp. 293-300. November 13, 1928.
- 1931. Fur-picking in monkeys as an act of adornment. Journ. Mamm., vol. 12, pp. 430-431. November, 1931.
- WADE, 1927. Breeding habits and early life of the thirteen-striped ground squirrel, *Citellus tridecemlineatus* (Mitchill). Journ. Mamm., vol. 8, p. 270. November 11, 1927.
- WARNER, 1927. A study of sex behavior in the white rat by means of the obstruction method. Comp. Psych. Monogr., Baltimore, vol. 4, No. 22, pp. 1-68. July, 1927.
- WATT, 1931. Ovulation, oestrus and copulation with consequent dystocia during pregnancy, in the mouse. Science, n.s., vol. 73, pp. 75-76. January 16, 1931.
- WESTERMARCK, 1927. History of Human Marriage. Revised Edition. 3 vols. The Allerton Book Co., New York.
- WIGHT, 1931. Reproduction in the eastern skunk (*Mephitis mephitis nigra*). Journ. Mamm., vol. 12, pp. 42-47. February, 1931.
- YERKES, 1927. The mind of a gorilla: Part II. Mental development. Genetic Psych. Monographs, Worcester, vol. 2, No. 6, pp. 381-551. November, 1927.
- 1928. The mind of a gorilla: Part III. Memory. Comparative Psych. Monographs, Baltimore, vol. 5, No. 2, pp. 1-92. December, 1928.
- ZEDTWITZ, 1930. Beobachtungen im Zoologischen Garten Berlin. Zool. Garten, Leipzig, n. F., vol. 2, pp. 278-285. March, 1930.
- 1930. Neues aus dem Zoologischen Garten

- Berlin. Zool. Garten, Leipzig, n. F., vol. 4, pp. 13-16. February, 1931.
- ZUCKERMAN, 1929. The social life of the primates. *The Realist*, London, vol. 1, pt. 2, pp. 72-88. July, 1929.
- 1930. The menstrual cycle of the primates. Part I. General nature and homology. *Proc. Zool. Soc. London*, pt. 3, pp. 691-754. October 22, 1930.
- ZUCKERMAN, 1931. The menstrual cycle of the primates, Part III. The alleged breeding-season of primates, with special reference to the Chacma baboon (*Papio porcarius*). *Proc. Zool. Soc. London*, pt. 1, pp. 325-343. April, 1931.





HAPLOIDY IN METAZOA

By FRANZ SCHRADER AND SALLY HUGHES-SCHRADER

Department of Zoology, Columbia University

INTRODUCTION

THE origin of haploidy in Metazoa, its bearing on the problem of sex determination, and indeed the very existence of haploid individuals have long been the subject of much cogitation. As one or all of these questions have presented themselves in various fields of biology, different investigators have endeavored to explain the moot aspects, each from his own point of view. As a result there is available a conglomeration of hypotheses. To admit that few of these are worth consideration, and none is entirely satisfactory is in itself an appreciation of the difficulties involved. The subject as a whole has repeatedly presented itself in our work on the cytology of the coccids, and the present review has been written not only with the intention of critically evaluating the more important of the various hypotheses but also of discussing the possible bearing that certain features of coccid cytology may have on the question.

The central point of interest lies in the fact that so far as is known, all haploid animals are males. The present brief survey of the various attempts to throw light on this peculiarity and the related facts which it involves does not endeavor to go back beyond the period when the rôle played by the nucleus in the mechanism of heredity first became fully realized.

HYPOTHESES OF HAPLOIDY

Older hypotheses

Perhaps the first to consider the status of haploid individuals in this period was

von Lenhossék ('03), who suggested that the queen bee carries two kinds of eggs, one of which is of a female and the other of a male type. Only the former can be fertilized, and, indeed, requires fertilization before development can occur; whereas the male type of egg develops parthenogenetically and is perhaps not fertilizable in any case. Buttel-Reepens in the very next year subjected this hypothesis of a progametic sex determination to a thorough criticism which practically eliminated it from consideration, and genetic and cytological investigations have since that day supported Buttel-Reepens. However, the ideas expressed by von Lenhossék have since reappeared in the literature several times (thus Godlewski, '13).

In 1905 and 1906 R. Hertwig proposed his hypothesis of the karyoplasmic ratio, and in the course of its elaboration also considered the question of the production of haploid males. According to Hertwig, when the eggs of the bee develop parthenogenetically after reduction there must occur a readjustment of the nuclear volume of such proportions that a karyoplasmic ratio characteristic of maleness results. But in 1912 he abandoned the hypothesis in so far as it pertained to sex determination in general and haploid parthenogenesis in particular. Indeed, shortly after this Nachtsheim ('13) and Oehninger ('13) reported the nuclear volume to be very much the same in corresponding organs of the two sexes. This of course does not eliminate the possibility that the cytoplasmic volume of female cells differs from that of male cells, which in itself would furnish a basis for a difference in

karyoplasmic ratio. However, in an entirely different insect, *Icerya purchasi*, Schrader and Hughes-Schrader ('26) have shown that even where there is a difference in the volume of chromosome material between the two sexes, the cytoplasmic volume varies proportionately. But it must be recognised that exact measurements are very difficult to make, and that a very slight difference between female and male cells may conceivably escape unnoticed, although possibly of the utmost importance in the process of sex determination. But even though it must thus be admitted that the volumetric relationship of nucleus to cytoplasm may possibly play some rôle in the question, we are not in a position to utilize the suggestion at the present moment.

Chromosomal hypotheses

This brings us to a consideration of hypotheses involving chromosomes, both from the cytological and the genetical points of view. The first of these met all the objections that had been voiced against the earlier hypotheses and rested on the original form of the sex chromosome hypothesis. As broached by Wilson ('09) and Nachtsheim ('13) it may be given briefly as follows. Each X chromosome carries a definite quantity of some substance, which we may call sex chromatin. The total quantity of sex chromatin present in the developing egg determines whether a male or a female is produced. Thus two X chromosomes contain the quantity of sex chromatin which will bring about female development; one X the quantity that results in male development. This would explain not only the normal type of sex determination of diploid animals in which females are characterized by the chromosome formula $2A + 2X$ and males by $2A + 1X$ (when A = one haploid set of autosomes), but

also furnishes a simple explanation for the fact that haploid individuals are always male. For evidently if only the X chromosomes and not the autosomes are primarily responsible for the character of the sexual development, an egg which develops parthenogenetically after the reduction division has left it with only one X, would automatically give rise to a male.

The further development and elaboration of this older sex chromosome hypothesis culminated in the theory of sex determination which is embodied in the conclusions of Goldschmidt and Bridges. The chief departure of this modern theory from its progenitor lies in the recognition that autosomes as well as sex chromosomes are concerned in sex determination and that in effect the whole process rests on genetic factors just as does the development of any other character. Since in the case of *Drosophila* it so happens that the total effect of the genes concerned with sex determination carried by the X chromosome is to push development in the female direction, whereas that of the corresponding autosomal genes is toward maleness, sex determination may be said to rest on the ratio of the number of X chromosomes to the number of haploid sets of autosomes, which in turn may be expressed as a quotient. If this quotient is 1 or greater, femaleness is indicated; if it is .5 or less, maleness.

But although this modification of the older sex chromosome hypothesis has been triumphantly successful in meeting all the newer cytological and genetic data, it has also thrown open once more the old puzzle of sex determination in haploid individuals. For manifestly, a haploid *Drosophila* would have the formula $1X + 1A$, and the quotient in that case would be 1, just as it is in the normal female of the species. Therefore if such a *Droso-*

phila were viable (which apparently it is not) one would expect it to be a female and not a male, as is the case with all known haploid animals.

Bridges' subsidiary evidence ('25a, '25b, '30) does indeed suggest that in *Drosophila* this expectation would actually be realized. Thus in certain mosaics, circumscribed regions of the fly are composed of cells which have lost most and possibly all of the chromosomes of one haploid set, and such regions appear to be female in character. If, for instance, an area of this type includes the front leg, the sex comb, which is characteristic of males only, will be absent. Now it must be recognized that the demonstration is not complete, for Bridges has not been able to show that the complete haploid set of chromosomes has been eliminated from the cells of the regions in question, but the general tendency of these findings is certainly in support of his general conclusion. But, if anything, this makes the fact that in all other cases haploid individuals are always males, only a still greater puzzle.

Schrader and Sturtevant ('23) suggested that a compromise may be brought about in the following way. If X be given the arbitrary value of -6 , and A the value of $+2$, and if it is further assumed that the threshold value for femaleness is at -7 and for maleness at -5 , then it is possible to regard the effective relation as an algebraic summation of the two types of chromosomes. (Apparently Witschi ('29) has taken this to mean that algebraic sums on the minus side of 0 connote femaleness and those on the plus side maleness. This is of course a misunderstanding of the hypothesis. As indicated above, the direction of sexual development depends on which side of the threshold values the algebraic sum falls. Since the present paper was sent to press Klingstedt (Act. Zool. Fenn. 10) has made a similar criticism of Witschi's interpretation.) In

other words, with these arbitrary values, a preponderance of seven units of femaleness would bring about normal female development, whereas a preponderance of only five units would result in maleness. A comparative tabulation of the genic balance hypothesis of Bridges and the algebraic sum hypothesis side by side will show at a glance the relationship of the two (Table 1).

It will be seen that the algebraic sum hypothesis will account for the fact that haploid individuals are males, whereas the genic balance hypothesis does not. Bridges has, however, objected that, so far as *Drosophila* is concerned, the appli-

TABLE 1
Sex types of Drosophila analysed according to the algebraic sum and the genic balance hypotheses of sex determination

NAME	CONSTITUTION	ALGEBRAIC SUM	GENIC BALANCE
Super-male.....	$X + 3A$	0	0.33
Male.....	$X + 2A$	-2	0.5
Haploid.....	$X + 1A$	-4	1.0
Intersex.....	$2X + 3A$	-6	0.66
Diploid female.....	$2X + 2A$	-8	1.0
Triploid female.....	$3X + 3A$	-12	1.0
Super-female.....	$3X + 2A$	-14	1.5

cability of the algebraic sum hypothesis is dubious because the numerical differences between the successive types do not correspond very well to the actually observed differences in the sexual characters of the flies of the different types. Thus there is a difference of eight units between the diploid and the tetraploid females, which in actuality show practically no difference in their sex characteristics, whereas only six units indicate the striking difference between the females and the males. Since the genic balance hypothesis accounts for such differences very well, the algebraic hypothesis is manifestly at a disadvantage until further evidence is brought out in its support.

Unlike Bridges, Goldschmidt ('20) has included in his considerations the question of sex determination in haploid individuals. Utilizing certain conclusions derived from his crosses of Lepidoptera, he suggests that the genes for maleness (MM) impress their effect upon the egg before maturation and hence all eggs are alike in their male tendency. The X-chromosome carries one or more genes for femaleness (F). If the relationship is $FF > MM > F$, then an explanation for the maleness of haploid individuals is at hand, since the number of X chromosomes depends on whether the egg has been fertilized or not. If fertilized, two X are present and the female tendency thereby dominates the male tendency. But if not fertilized, only one X is carried in the egg and then the male tendency gains the upper hand. Goldschmidt's hypothesis thus makes due allowance for the existence of haploid males. It need hardly be said that it would at once gain the utmost importance if further light could be thrown on the rôle that Goldschmidt ascribes to the cytoplasm.

Other hypotheses

No immediate solution of the difficulties involved in the problem is to be expected from the suggestions recently made by some other workers. Thus Witschi ('29) has suggested that since the diploid individuals in our cases are always females, the factors for femaleness must there be epistatic to those for maleness (i.e., $FF > MM$). But since haploid animals are always males, the explanation may rest on the fact that the haploid state in some way changes the conditions obtaining in the diploid individuals and thus $M > F$. It may well be assumed that if such a reversal of epistasis is responsible for the maleness it in turn is due to physiological conditions obtaining in haploid in-

dividuals. But that, of course, is not an explanation and merely serves as a basis for the opinion that a final elucidation must rest upon an experimental analysis of such physiological conditions. Indeed Witschi himself is free to state that he regards this interpretation merely as a suggestion for further work.

Nor does Castle's recent proposal ('30) that the interpretation of several workers on sex determination in lower plants be applied to animals offer immediate help, and this despite the fact that Castle had haploid animals especially in mind. As is well known, the interpretations just mentioned are based on the supposition that sex differences are merely plus and minus variations in a single scale of gradations in sexual character. In the sex determination of animals like *Drosophila* we are dealing with two types of individuals, those with a plus and those with a minus tendency, or male and female respectively. The mature eggs all being alike in carrying the plus tendency, the production of two sexes must of necessity rest upon the existence of two kinds of sperm. As is already well known, this differentiation rests on the so-called X Y chromosomes, the X being considered as a chromosome with a plus or female tendency, while the Y is neuter or else of a minus tendency. All that is of course nothing more than a slightly different way of stating what we already know. But it is quite clear that on this basis, if an egg is not fertilized and develops parthenogenetically it can carry only the plus or female tendency. In other words, Castle encounters exactly the same difficulty as does Bridges in the latter's conception of the genic balance hypothesis, for according to this view a haploid individual should be female and not male.

Castle is of course aware of the difficulty and endeavors to escape the dilemma by

suggesting that in such a haploid individual "its feeble haploid state (perhaps) causes it to form sperms rather than eggs but these sperms transmit the plus sex-tendency for which the mother was homozygous." The hollowness of this explanation is manifest, and indeed seems to be apparent to Castle himself, for a few lines farther on he writes as follows: "What makes these haploid individuals somatically male (producers of sperm rather than eggs), we are at present unable to state. Genetically they are female; phenotypically or somatically only are they male." Needless to say the sentences just quoted are tantamount to a concession that we are just where we were before.

In brief, none of the present hypotheses is fully satisfactory. Of them all, only Goldschmidt's and Schrader and Sturtevant's will cover both diploid and haploid males. The former of these is in urgent need of further elucidation of the basic assumption that maleness can be impressed upon the cytoplasm of the egg before fertilization, whereas the latter offers a conflict with the genic balance hypothesis which affects at least its general applicability.

OCCURRENCE OF HAPLOIDY IN METAZOA

Criteria of haploidy

Before considering our own suggestions in their relation to the various aspects of the problem of haploidy, it may not be amiss to take stock of our present knowledge concerning the occurrence of species with haploid males. Although the number of species in which haploidy occurs is probably much larger than was formerly thought, a satisfactory demonstration of its existence has so far been given in relatively few instances.

It must be realized that such a demonstration cannot be made without cyto-

logical evidence. Breeding experiments alone may well establish that females are capable of producing young without fertilization by a male and that the young so produced are invariably males. Again, genetic evidence may show that such offspring are always homozygous. But neither the one nor both of these findings is sufficient for a demonstration of haploidy, for such evidence in no wise precludes the possibility that diploidy has been restored to the developing egg by any one of several methods. Thus the eggs might undergo a reduction division and, if this were followed by a separation of the equational halves of the chromosomes unaccompanied by a cytoplasmic division, development would take place in a homozygous condition but with the diploid instead of the haploid complement of chromosomes.

Indeed, if cytological evidence to the effect that the eggs actually do undergo a normal reduction be added to the genetic evidence, haploidy is still not necessarily implied. Thus in the facultatively parthenogenetic race of *Lecanium* studied by Thomsen ('27), all eggs undergo a normal maturation, but diploidy is restored to the unfertilized eggs by the secondary union of the second polar body nucleus with the female pronucleus. Were the first maturation division reductional in this case, the parthenogenetically produced young might be homozygous for characters heterozygous in the mother, and still have been diploid throughout their entire development.

Similarly, if Tauson's ('27) evidence on *Asplanchna intermedia*, and Doncaster and Cannon's ('29) on *Pediculus*, are to be believed, an investigation of the spermatocytes need not in itself give a decisive test for the presence or absence of haploidy, for a precocious reduction may occur earlier, as in the spermatogonial cells.

TABLE 2

Forms in which the haploidy of males has been completely demonstrated. Abbreviations as follows: clv.—cleavage, dip.—diploid, div.—division, embr.—embryos, hap.—haploid, mat.—maturation, nucl.—nucleus, oog.—oogonia, pronucl.—pronucleus, soma.—somatic cells, spcyt.—spermatocyte, spg.—spermatogonia, spid.—spermatid

SPECIES	BREEDING DATA	NON-MEIOTIC CHROMOSOMES		MEIOSIS		REFERENCE	REMARKS
ACARINA		♀	♂	♀	♂		
1. <i>Tetranychus bimaculatus</i>	Virgin ♀ → ♂♂ only Mated ♀ → ♂♂ & ♀♀	6 in fusion nucl., clv. nucl., embr., & soma. of nymphs.	3 in ♀ pronucl., clv. nucl., embr., & soma. of young nymphs.	2 mat. div. → hap. pronucl.	Probably one div. only—equational. No reduction div.	Schrader, '23	Meiotic div. not distinguishable from spermatogonial. Last div. before spid. formation is equational.
ALYRIDAE							
2. <i>Aleurodes lotella</i>	Virgin ♀ → ♂♂ only Mated ♀ → ♂♂ & ♀♀	26 in fusion nucl., clv. nucl., & soma. of larvae.	13 in ♀ pronucl., clv. nucl., embr., & soma. of larvae, spg. circa 13.	2 mat. div. → hap. pronucl.	One div. only, equational.	Thomsen, '27	Spicyt. div. is distinguishable from spg. div.
3. <i>Trialeurodes vaporariorum</i>	Virgin ♀ → ♂♂ only Mated ♀ → ♂♂ & ♀♀	22 in clv. nucl., embr. & soma. of pupae, oog. circa 22.	11 in clv. nucl., embr. & soma. of pupae, spg. circa 11.	2 mat. div. → hap. pronucl.	Probably one div. only—equational. No reduction div.	Schrader, '20; Thomsen, '27	Meiotic div. not distinguishable from spermatogonial. Last div. before spid. formation is equational.
COCCIDAE							
4. <i>Echiniterys anomala</i>	Virgin ♀ → ♂♂ only Mated ♀ → ♂♂ & ♀♀	4 in clv. nucl., embr., oog., & soma. of all instars.	2 in clv. nucl., embr. spg., & soma. of all nymphal instars.	2 mat. div. → hap. pronucl.	One div. only, equational.	Hughes-Schrader, '30	
5. <i>Icerya litoralis</i>	Virgin ♀ → ♂♂ only Mated ♀ → ♂♂ & ♀♀	4 in clv. nucl., embr., oog., & soma. of all instars.	2 in clv. nucl., embr. spg., & soma. of all nymphal instars.	2 mat. div. → hap. pronucl.	One div. only, equational.	Hughes-Schrader, '30	

6. <i>Icerya montsen-ratusis</i>	Virgin ♀ → ♂♂ only Mated ♀ → ♂♂ & ♀♀	4 in clv. nucl., embr., oog., & soma. of all instars.	2 in clv. nucl., embr., spg., & soma. of all nymphal instars.	2 mat. div. → hap. pronucl.	One div. only, equational.	Hughes-Schrader, '30	
7. <i>Icerya purchasi</i>	Unmated ♂♂ → ♂♂ & ♀♀ Mated ♂♂ → ♂♂ & ♀♀	4 in fusion nucl., clv. nucl., embr., oog., & soma. of all instars.	2 in ♀ pronucl., clv. nucl., embr., spg., & soma. of all nymphal instars.	2 mat. div. → hap. pronucl.	One div. only, equational.	Pierantoni, '12, '14; Hughes-Schrader, '25, '26, '27; Schrader & Hughes-Schrader, '26	
HYMENOPTERA							
8. <i>Apis mellifica</i>	Virgin ♀ → ♂♂ only Mated ♀ → ♂♂ & ♀♀	32 in 1st clv. nucl. & embr.—may break up into 64 in late embr. & reunite into 16 in oog.	16 in 1st clv. nucl., & embr.—may break up into 32 or 64 in late embr. Spg. 16.	2 mat. div. → hap. pronucl. of 8 double chromosomes	First div. abortive. Second div. equational & unequal. Only one spid. is functional.	Petrunkewitsch, '01; Meves, '04, '07; Doncaster, '06, '07; Mark & Copeland, '06; Nachtsheim, '13	All data from Nachtsheim. No agreement among authors as to counts or meaning.
9. <i>Paracapsidomopsis floridanus</i>	Virgin ♀ → ♂♂ only Mated ♀ → ♀♀ only with occasional mixed broods.	16 in clv. nucl., embr. & soma.	8 in spg. & soma.	2 mat. div. → hap. pronucl.	First div. abortive. Second div. equational & equal. Both spids. functional.	Patterson, '17, '21; Patterson & Porter, '17; Patterson & Hamlett, '25	Report ♂ soma. "hap. with variations" which are unexplained. Haploidy established for ♂♂ of mixed as well as unisexual broods.
10. <i>Peromidea ribeisi</i> (= <i>Nematus ribeisi</i>)	Virgin ♀ → ♂♂ only Mated ♀ → ♂♂ & ♀♀	16 in oog., circa 16 in fusion nucl., embr. & soma.	8 in embr. & soma.	2 mat. div. → hap. pronucl.	First div. abortive. Second div. equational & equal. Both spids. functional.	Doncaster, '06, '07; Peacock & Sanderson, '31	All data from Peacock & Sanderson. Variability in counts of ♀ soma. & pairing of oog. chromosomes suggest "Sammalebranosom." Evidence for first div. inadequate.

The ensuing meiosis may be, therefore, of the haploid type, although the males are somatically diploid.

Finally, the possibility that haploid nuclei may double their chromosomes at some stage is always to be considered. Paula Hertwig ('20) suggested such a possibility in her consideration of haploidy in bees, and indeed just such a restoration of diploidy has since been discovered in the parthenogenetically produced frogs studied by Parmenter ('20, '25, '26). In these cases the regulation from haploidy to diploidy may occur over a considerable developmental period; only those individuals surviving, apparently, which successfully assume the diploid condition.

Thus in a given case the knowledge that males only are produced parthenogenetically from reduced or haploid eggs, and that the meiosis of the males evinces those peculiarities conditioned by the presence of but one haploid set of chromosomes, may strongly support the hypothesis of haploidy, but does not in itself prove it. The final proof must include a demonstration of haploidy in the somatic cells of the most important developmental stages of the male from egg to adult. It is with this strict but nevertheless fair criterion of haploidy in mind that we present the following analysis of the various reputed cases of haploidy among the metazoa. Fully conforming to our requirements for haploidy are the cases brought together in Table 2.

Fully established cases

It will be seen from Table 2 that in at least seven species (numbers 1 to 7 inclusive) the evidence for male haploidy is absolutely conclusive. In the three other species (all Hymenoptera) also included in Table 2 we believe the existence of haploidy to be established, but in none of these cases is the demonstration so un-

questionable as in the former group. In Peacock and Sanderson's ('31) study of the saw-fly, *Pteronidea ribesii*, the most exacting criteria for haploidy would seem to have been met. But even here the chromosomes of the female line show some indication of a compound character (note the variation of the somatic counts in female embryos, and the pairing of the oogonial chromosomes). However, these variations seem in no wise to affect the chromosomes of the male line nor the basic relation between the chromosomes of the two sexes. Again, the case for haploidy in *Paracopidosomopsis* is weakened, although probably not materially, by Patterson and Porter's ('17) preliminary report of the occurrence of variations in the haploid counts in male somatic cells, variations which the authors have neither described nor explained in subsequent publications. Finally in the classic case of the bee, although Nachtsheim's studies have unified the conflicting reports of the many previous workers and make the haploidy of the males almost certain, the evidence may still be questioned at certain points. Thus it has been suggested (P. Hertwig, '20; Vandel, '31) that the formation of compounds or "*Sammelchromosomen*" may mask a restitution of diploidy in some developmental stage in the haploid male. This might be followed by a reduction to haploidy in the spermatogonial cells of the male. Following such assumptions (for which, it must be remembered, positive cytological evidence is quite lacking), neither the typically haploid character of the male meiosis nor the development of males from unfertilized, reduced eggs would constitute adequate evidence for the haploidy of the males, which might still be diploid during the major part of their lives. Some skepticism is perhaps justified on the grounds of the admittedly involved chro-

mosomal behavior and the highly unfavorable nature of the material for a convincing cytological analysis. In such a case the critical judgment of so skilled an observer as Nachtsheim carries more than ordinary weight, and the present authors believe his final conclusion for male haploidy to be justified.

Incompletely established cases

Table 3 brings together seven species, in each of which some cytological evidence for male haploidy is available, but in none of which has a satisfactory demonstration been accomplished. *Vespa crabo*, *Vespa maculata*, *Camponotus herculeanus*, and *Xylocopa violacea* all evince a typically haploid meiosis in the male, but data on female meiosis, on the results of breeding, and, what is especially pertinent, somatic counts in the two sexes, are either entirely lacking or quite inadequate to establish the haploidy of the males from egg to adult. *Dryophanta erinacei* is in the same situation; its case is further complicated by the fact that the only chromosome count available for the female is approximately the same as those found in the male. For *Pteronidea melanoplus* the breeding data and the type of male meiosis suggest haploidy of the males, but the absence of data on the meiosis of the egg and on the somatic chromosomes precludes a positive conclusion. In *Crypticerya rosae*, on the other hand, somatic haploidy is established for half the embryos and first instar nymphs, female diploidy is also proved, and the reduction of all eggs is very probable; lacking are late nymphal and adult male counts, and the character of the meiosis in the male.

There remains a group of species for which haploidy has been claimed on cytological grounds but in regard to which no conclusion is at present justified. The gall-fly *Neuroterus lenticularis* (Doncaster,

'10, '11, '16) belongs in this category. On the basis of Doncaster's studies it is probable that the male meiosis is of the same haploid type exemplified by *Paracopidosomopsis* and *Vespa*, and that the eggs of certain females (presumably male-producers) undergo a chromosome reduction, but the observations on the chromosome cycle are too confused and contradictory to warrant any conclusion. Similarly, in *Osmia cornuta*, Armbruster found but one meiotic division in the male germ cells,—evidence of possible haploidy. Armbruster's claim that this division is reductional in character has not been confirmed, and it is probable that the apparent reduction, as well as his conflicting chromosome counts in male somatic cells, depends upon some sort of compound chromosome formation. The parasitic wasp, *Habrobracon brevicornis*, must also, for the present at least, remain in the unproved category. In 1918 P. W. Whiting made a preliminary announcement on the cytology of this wasp in which he states that the males are haploid and that one of their meiotic divisions is abortive. A. R. Whiting ('27a, '27b) confirms these general statements and adds that the second meiotic division in the male is equational and equal, and that the chromosome number is approximately 11 in the male and 22 in the female. So far, however, the cytological findings on which these claims are based have not been published and it is accordingly impossible to judge whether somatic and meiotic haploidy is actually established. A suspended judgment is especially advisable here in view of the genetic evidence for the existence of bi-parental or diploid males in this species (A. R. Whiting, '27a, '27b). The cytology of these aberrant males has not been reported beyond a statement to the effect that their meiosis seems to resemble, in the presence of an abortive first division, that of the uni-

TABLE 3
Forms in which the cytological evidence for male haploidy is incomplete in from one to almost all respects. Abbreviations as in Table 2

SPECIES	BREEDING DATA	NON-MEIOTIC CHROMOSOMES		MEIOSIS		REFERENCE	REMARKS
		♀	♂	♀	♂		
COCIDAE 1. <i>Crypticarya rosae</i>		4 in clv. nucl., embr., 1st instar larvae, & soma. of adult.	2 in clv. nucl., embr., & 1st instar larvae.	Stages incomplete, but 2 mat. div. indicated.		Hughes-Schrader, '30	Somatic haploidy of ♂♂ not completely proved; ♂ meiosis lacking.
HYMENOPTERA 2. <i>Camponotus herculeanus</i>					First div. abortive. Second div. equational & equal. Both spstds. functional.	Lams, '08	Hap. type of ♂ meiosis only evidence for ♂ haploidy.
3. <i>Dryophanta erinacei</i>		13 or 14 in follicular cells of ovary.	12 in soma.		First div. abortive. Second div. equational & equal. Both spstds. functional.	Wieman, '15	Follicular counts known to be variable in other species; hap. type of ♂ meiosis only evidence for ♂ haploidy.
4. <i>Pteronidea melanoplus</i> (= <i>Nematus melanoplus</i>)	Virgin ♀♀ → ♂♂ only Mated ♀♀ → ♂♂ & ♀♀		8 in spg.		First div. abortive. Second div. equational & equal. Both spstds. functional.	Peacock, '25; Peacock & Sanderson, '31	All data from '31 paper, which corrects '25 account of 2 equational divs. Somatic chromosomes of ♂ & ♀ lacking.

5. <i>Vespa crabro</i>					First div. abortive. Second div. equational & equal. Both spstds. functional.	Meves & Duesberg, '08	Hap. type of ♂ meiosis only evidence for ♂ haploidy.
6. <i>Vespa maculata</i>					First div. abortive. Second div. equational & equal. Both spstds. functional.	Mark & Copeland, '07	Hap. type of ♂ meiosis only evidence for ♂ haploidy.
7. <i>Xyllocopa violacea</i>		32 in first clv. nucl. in some eggs, presumably ♀-producing.	16 in first clv. nucl. in some eggs, presumably ♂-producing.		First div. abortive. Second div. equational & unequal. Only one spstd. functional.	Granata, '09, '13	Somatic determinations incomplete, & all data for ♀ lacking.

parental or haploid males,—a finding which, if confirmed, can only increase the need for a complete cytological study. The verdict of unproved must be passed also upon Patterson's ('28a, '28b) claim for male haploidy in the various species of Cynipidae which he has investigated, since no cytological evidence has as yet been published relative to these species.

Despite the unanimity with which previous writers have placed the rotifers in such lists, we do not regard haploidy as established there. The data from breeding experiments and the cytological evidence are sufficient to establish the fact that sexual eggs may develop parthenogenetically after giving off two polar bodies, and that such eggs always give rise to males. But no conclusive evidence is available to show that the haploid number is actually maintained. Indeed the reports of the different investigators are so much at variance with each other that it seems a matter of surprise that any final conclusion has been based on them at all. To justify this critical attitude, it may be well to review very briefly the investigations that have been made on the two genera, Hydatina and Asplanchna.

In *Hydatina senta*, Lenssen ('98) gave the diploid number as 10 or 12. In 1909 Whitney reported it as between 20 and 30, giving the haploid number as from 10 to 14. But Shull in 1921 concluded that the diploid number is 12. It will be seen that, far from establishing the fact that the males are haploid, these data do not even permit a conclusion on the diploid number.

In *Asplanchna intermedia*, Whitney ('24) reported 52 chromosomes in the female and 26 in the mature sexual egg (which gives rise to a male if unfertilized). In the same year Tauson reported the diploid number in the same species to be 24 and emphasized her conclusion that the male is not haploid. However in 1925 Wiggernhorn

and Whitney supported Whitney's earlier findings with the claim that somatic cells of female embryos carry about 51 chromosomes, whereas those of males show 25 or 26. But Tauson in 1927 reiterated that the diploid number is 24 and that males are diploid and not haploid. Finally in 1929 Whitney conceded that he had misinterpreted some of the stages but did not specify in what respects he had been in error. Manifestly a final conclusion is even less justified here than in the case of Hydatina.

Nor do the remaining cytological studies on rotifers settle the question. In his apparently reliable investigation of *Asplanchna amphora*, Whitney ('29) found that the diploid number is 26 and that males are haploid. It is consequently somewhat of a surprise to read his statement that "as the chromosome cycle is very similar to, if not identical with, that of *Asplanchna intermedia*, most of the important features of Tauson's work have been confirmed," for certainly the two investigations come to no agreement on the fundamental questions of haploidy. Again, Storch's work ('24) on *Asplanchna priodonta* led him to the conclusion that the diploid number is 16 and that the unfertilized egg begins its parthenogenetic development with 8 chromosomes. (Whitney ('29) objects that certain of Storch's figures show 40 to 49 chromosomes, but he has overlooked Storch's explanation that such figures were drawn from total preparations. In these, according to Storch, the relatively long chromosomes cross and overlap each other at many points and at such localities present areas of refraction which simulate a high number of chromosomes.) But Storch was not primarily interested in the question of chromosome number, and his findings will hardly suffice to settle the matter.

No special mention need be made of the

investigations of the spermatogenesis of various rotifers except to indicate that there also no agreement has been achieved.

In judging all these findings it is only fair to acknowledge that the group presents the utmost difficulties to cytological work. But plainly, on the basis of such reports as we have reviewed, a judicial skepticism is called for, even though it seems probable that male rotifers will eventually prove to be haploid, as almost everyone now assumes.

THE COCCIDAE IN RELATION TO HAPLOIDY

Analysis of problem

There is a strong possibility that the problem of haploidy is more complex than a statement of its central point,—i.e., why are haploid individuals always male?—would suggest. The historical hypotheses of haploidy hold in common the idea that the process of sex determination in haploid individuals differs from the more usual type only in some simple or perhaps single respect. It may therefore be pertinent to suggest that the differences between the two types may well be more far-reaching and that they have not been attained in a single step. The problems which are probably involved may conveniently be placed under three headings.

1. In the first place it must be recognised that so far as we know animals which normally are diploid in both sexes do not produce viable haploid offspring. Eggs with only the haploid complement of chromosomes have been known to begin development, but never does such development go beyond the very early stages without some type of adjustment of the chromosome number. No haploid individual has ever been known to reach sexual maturity in such cases. This is especially well illustrated by researches

on frogs which have been produced through artificial parthenogenesis (Hovasse, '22; Parmenter, '20, '25, '26). Since species with haploid males have undoubtedly been derived from species in which they are diploid, certain changes must have occurred to make viability in the haploid state possible. It must also be recognized that the production of haploid individuals may not have been the result of a single accident of development, as is apparently the case in the plants mentioned below, but may represent the culmination of a whole series of minor changes. The latter possibility we believe to be exemplified by certain species of coccids.

2. Among the higher plants, whose sporophytes are as fundamentally diploid in character as is the soma of the vast majority of metazoans, there appears to be no such block to the development of occasional haploid offspring. Thus haploid individuals of certain species of *Datura*, *Nicotianum*, *Oenothera*, *Triticum*, *Solanum*, and others have proved capable of developing to maturity with the single complement of chromosomes. But such haploid forms as these present another bar to the permanent establishment of haploidy in a species. This lies in the behavior of the single set of chromosomes during meiosis. In all the cases investigated the large majority of the pollen mother cells undergoes an irregular reduction division in which the chromosomes of the haploid group are distributed at random to the two poles. Very few male gametes therefore receive the full haploid set and become normal pollen grains. In the others the number of chromosomes may of course vary from zero to the haploid number, and such gametes are rarely if ever functional. The maintenance of the race must rest in such cases on precariously few gametes. In other words, in the evolution of a species with haploid males, the meiotic

divisions in the latter must become subject to some regulatory factor which either sends the complete haploid set of chromosomes to one pole in the reduction division, or else eliminates reduction altogether. The haploid sporophytes of the plants mentioned have not successfully overcome this second block to a permanent haploidy.

3. Even if, through the agency of such a regulatory factor, a majority of the male gametes should become functional, another obstacle remains to be overcome. A brief consideration will make it evident that since all such viable gametes of haploid individuals carry the full haploid set of chromosomes, the ensuing fertilization will at once restore the diploid number of chromosomes, and therewith haploidy disappears once more. In order to avoid this, a further change relative to the physiology of the eggs must occur to make the continuous production of haploid individuals possible. This might happen in a variety of ways. Thus apyrene sperm, or sperm carrying no chromosomes, might be produced which would nevertheless retain the ability to activate the egg; or the eggs not reached by sperm might become directly capable of independent or parthenogenetic development. However investigated, the induction of parthenogenetic development in the eggs is a third essential step in the origin of haploidy.

4. The three foregoing considerations are concerned with the mode of origin of haploidy. It will be seen that the central point of why such haploid individuals should always be of the male sex still remains. It is, however, more than probable that with a complete elucidation of the origin of haploidy this final question will be automatically answered. If our conclusions still fall short of that desideratum it must be realized that the defect lies in the fact that our analysis of

the origin of haploidy is still incomplete. However, in so far as these investigations offer an approach to the central objective, they may have accomplished something toward its final solution.

Acquisition of viability in the haploid state

Within the group of the coccids are represented both beginning and end stages in the establishment of haploidy. Thus in all the iceryine coccids thus far studied cytologically, the haploidy of the males has been completely established. In all five species (representing three genera of this tribe) the cytological conditions are exceptionally clear and convincing; the females are diploid with a chromosome number of 4, and the males in every case haploid with the reduced chromosome number of 2. The viability of haploid individuals is, in these species, beyond any question. At the other extreme we find species, such as *Llaveia* and *Protortonia*, in which both sexes are invariably diploid. The expectation of finding species, within this group, representative of intermediate stages does not, therefore, seem entirely unjustified. But in no case, in the course of considerable breeding and cytological examination of *Protortonia* and other diploid species, has an occasional or accidental haploid form ever been encountered. In these very same cases, however, there lies indirect evidence that the ability to develop and to survive in the haploid condition is in process of acquisition by the male sex, not, as might at first be expected, by the sudden or accidental parthenogenetic development of a mature egg, but by a series of changes in the chromosomal conditions of the diploid males themselves. The evidence for this hypothesis lies in an apparently progressive degeneration in one-half of the chromosomes of the male. Different stages in this process are exemplified by different species, and it is pos-

sible so to arrange these species as to illustrate a series of steps which may have been taken in the passage from diploidy to haploidy. The basic phenomenon, as indicated above, is a gradual degeneration of one haploid set of chromosomes in the male; the process is reflected chiefly in the behavior of the chromosomes during meiosis, but in its later stages the soma also is affected.

In ordinary cases the stability and permanence of the diploid condition is dependent upon the regularity of pairing (pseudoreduction) between homologous chromosomes and the ensuing reduction in the meiotic divisions of the germ cells. In turn this pairing may be looked on as an indication that the members of the pair are homologous, any decided difference in either member affecting the synaptic relation. It is not surprising, therefore, to find that it is precisely this feature of meiosis which is first impaired by the degenerative changes leading toward haploidy. It is recognized of course that such impairment or loss of synapsis in a diploid set of chromosomes may conceivably be due to one of several causes. That in the case of the coccids it is intimately associated with the progressive degeneration of one set of chromosomes, may be indicated, we believe, by the following considerations.

The starting point in the series, i.e., the normal diploid condition with no trace of a haploid tendency, is furnished by *Llaveia bouvari*. The chromosome cycle in this species is prototypal; both sexes are diploid, the female with six chromosomes, the male with five; these chromosomes are distinguishable as three pairs of differing size, the longest pair being represented by but one chromosome in the male group. In the meiosis of the male germ cells some 95 per cent of the primary spermatocytes show the occurrence of

pseudoreduction, or pairing between the members of the two pairs of autosomes. The prophase nucleus subdivides into three nuclear vesicles, in one of which the unmated heterochromosome evolves alone and precociously, undergoes an equational split, and condenses into a dyad. In each of the other two vesicles the two members of one autosomal pair of chromosomes are formed; each splits equationally and then pairs with its mate to form a tetrad. The two tetrads and the dyad divide equally at the first division. In the second division prophase the X-chromatid becomes attached to one end of the larger dyad, and in the ensuing division passes undivided to one pole, while the two autosomal dyads divide evenly. Thus two types of sperm are produced, male-determining with two chromosomes, and female-determining with three chromosomes. We would again emphasize the orthodox behavior of the chromosomes in this meiosis as probably representing the primitive or basic condition, in which the homology of the chromosomes is unimpaired and there is consequently a normal pairing and reduction.

A significant variation of this normal synapsis occurs in approximately 5 per cent of the primary spermatocytes of all the males of *Llaveia bouvari* studied, a variation which shows the beginning of the asynaptic habit. In these cells the two members of the smaller pair of autosomes evolve in separate vesicles; each one splits equationally and condenses into a dyad without any contact with its homologous chromosome. In the first division these two divide quite independently of each other. In the second division their derivative chromatids come together momentarily before passing to opposite poles. In other words, in some 5 per cent of the spermatocytes, one pair of chromosomes no longer undergoes the normal prophase

synapsis and tetrad formation,—an aberration which foreshadows the complete loss of synapsis in the males of the higher coccids and indicates the possible first step in those changes which we believe lead to the final degeneration and loss of one whole haploid set of chromosomes.

In *Protortonia primitiva* the progressive impairment of synapsis in the male line is much further advanced. The somatic chromosome situation resembles that in *Llaveia*; the females have a diploid set of six chromosomes, the males of five, of

cocious and exaggerated separation of their equational halves) as they line up into a row of four units prior to the division, no actual pairing or synapsis occurs even between these two chromosomes. The retention of the common vesicle, together with the persistence of some degree of contact between the chromosome mates, we interpret as remnants of an old synaptic behavior. Comparison with *Llaveia* strengthens this interpretation, for there in 95 per cent of the spermatocytes each chromosome pair evolves with-



















GENUS	TYPES OF PAIRING			TYPES OF SPERMATOZOEA	REMARKS
<i>Llaveia</i> 95 per cent					Normal pairing. Both types of sperm viable.
<i>Llaveia</i> 5 per cent					1 Normal tetrad. Degeneration in 1 autosome. Both types of sperm viable.
<i>Protortonia</i>					Degeneration in 1 autosome. Partial degeneration in 1 member of other pair of autosomes. Both types of sperm viable.
<i>Gossyparia</i>					Degeneration in 1 entire set of autosomes. Heterochromosome lost. One type of sperm viable.
<i>Isoceryx</i>					Complete loss of degenerate set of autosomes. Heterochromosome lost. Only one type of sperm formed.

FIG. 1. DIAGRAM SHOWING PROGRESSIVE DEGENERATION IN ONE HAPLOID SET OF CHROMOSOMES, AS ILLUSTRATED IN A SERIES OF DIFFERENT SPECIES

Tetrad formation indicated by partial merging of two spheres or chromosomes, and partial loss of synapsis by apposition without merging. Normal chromosomes black, partially degenerate chromosomes striped, and completely degenerate chromosomes white. Heterochromosome indicated by X.

which only the heterochromosome of the male and the corresponding pair of the female set, are distinguishable by their size. In the primary spermatocytes no pairing of the ordinary sort occurs. Four nuclear vesicles are formed. A single chromosome develops in each of three of them. In the fourth and largest vesicle, two chromosomes are formed, but except for a transient, possible, end-to-end contact between two of the four equational halves or chromatids of these (all the chromosomes in this division show a pre-

in a single vesicle and there undergoes a regular synapsis and tetrad formation. Similarly, the type of behavior found in the aberrant spermatocytes of *Llaveia*, with their individual vesicles for each of the members of one chromosome pair and the accompanying loss of synapsis by this pair, has become the invariable rule for all but one pair of the *Protortonia* chromosomes. These relations are graphically represented in figure 1, which gives in diagrammatic form the three metaphase configurations resulting from the three

types of chromosome behavior just described. It will be seen that the progressive loss of synapsis and the accompanying separation of the once homologous chromosomes is the basic factor underlying the differentiation of the three types, which thus represent three closely seriated stages in a common evolution.

Passing now to the case of *Pseudococcus*—the three species which have been investigated show such uniformity of chromosome behavior that they may be discussed as a unit—, we encounter a type in which asynapsis is fully established for all the chromosomes, in all the cells of the male germ line. The females show a diploid set of ten chromosomes, and, as in all the other cases, a completely orthodox behavior. The male diploid number is also ten, but one of the two haploid sets of chromosomes tends to remain partially condensed and clumped during the resting phases of the nuclei. In the primary spermatocytes this haploid set condenses in advance of the other set, and, after a first division equational in character for all ten chromosomes, the telophase nuclei still show a differentiation and segregation of the chromosomes into two groups, one clumped and one loosely aggregated. The second division effects a separation of these two haploid sets, one passing to each pole. The points pertinent to the present discussion are the complete absence of synapsis, and the associated lack of synchrony in the cyclic changes of form in the chromosomes of the two haploid sets. A third point of interest is the fact that the changes undergone by one haploid set of chromosomes are reflected in the somatic, as well as the germinal, cells of the males. That haploid set which condenses precociously and tends to clump and act as a unit in the meiotic divisions, may be recognized in the somatic nuclei of all except the earliest

developmental stages by similar although less strongly marked characteristics.

In *Gossyparia spuria* we find a still more radical change in one haploid set of chromosomes of the male. Moreover, in this case there is strong evidence that these changes are positively degenerative in character. As usual the female is a normal diploid, with a chromosome number in this case of 28. In the meiosis of the male germ cells the behavior of the two haploid sets of chromosomes is remarkably different. One haploid set shows a marked heteropycnosis in the primary spermatocyte prophases, and this is accompanied by a peculiar pairing of its chromosomes. This pairing is not, apparently, of a synaptic nature; the fact that it is preceded by no preliminary formation of chromosome threads, together with occurrence of slight variations in the numbers of the bivalents formed, indicates the aberrant character of the association. The second haploid set evolves more slowly in the primary spermatocyte prophases. Its chromosomes, strikingly enough, show no trace of pairing, and give every indication of a normal condition. The first division is equational in the sense that all fourteen of the chromosomes of the normal set and the seven bivalents of the heteropycnotic set all undergo division. The condensation of the heteropycnotic group is maintained throughout the interkinesis, and the second division effects the separation of this group from the normal one. Finally, and this point clinches the evidence for the degenerative nature of the peculiarities of the heteropycnotic chromosomes, those spermatid nuclei which receive them almost invariably disintegrate; only those spermatids which receive the normal haploid set of chromosomes form functional sperm. Among thirty individuals studied, only one showed any attempt on the

part of the degenerate nuclei at sperm formation; and in this case the sperm formed were of a highly abnormal type. This exceptional case adds weight to the conception that the heteropycnotic chromosomes represent a group which formerly formed sperm but which has lost this ability through progressive degeneration, for it may possibly represent the occasional persistence of a stage just prior to the condition reached by the majority of the *Gossyparia* males in the evolutionary process in question.

The peculiarities of the heteropycnotic chromosomes are not an exclusively meiotic phenomenon, but find expression in the somatic cells as well. The abnormality of one haploid set of chromosomes becomes visible somatically for the first time during the late blastula stage in the development of the male individual. From this point on, the heteropycnosis and persistent condensation and clumping of one group of chromosomes continue throughout both resting and division phases of the somatic nuclei. It thus seems highly probable that *Gossyparia* males are, therefore, haploid in effect from an early developmental stage on, due to the inactivation of one haploid set of their diploid chromosome complement.

Such a series of changes as we have outlined, indicating a progressive physiological inactivation of one chromosome set, would logically culminate in the complete morphological loss of this haploid set from the chromosome cycle of the male. This final stage is indeed realized in the coccids by various of the iceryine species (*Icerya*, *Echinicerya*, and *Crypticerya*). In these forms, as described earlier, the morphological haploidy of the males is completely established.

To summarize, we submit that the gradual establishment of asynapsis, followed

by increasing impairment of the synchronous functioning of the two haploid sets of chromosomes, is correlated with the progressive degeneration and final loss of one set of chromosomes. Ability to survive in the haploid state may thus be in process of acquisition by the males of certain species of coccids, as it is already attained by others. A diagrammatic representation of the possible steps involved in this process as illustrated by the different species of coccids just discussed is shown in figure 1. It cannot be too strongly emphasized that this scheme attempts no expression of the phylogenetic relations of the various coccid species involved. This is indeed obvious, since *Icerya*, here regarded as a possible final stage, is certainly far more primitive, and more closely allied to such basic forms as *Llaveia*, than are the highly specialized species of the *Gossyparia* and *Pseudococcus* groups. The evidence is rather to be interpreted to the effect that some such development as we have traced is taking place in different groups of coccids, but evidently at different rates, and probably in different ways, in different groups. Thus in the specialized *Lecanium* species studied by Thomsen ('27)—the males in these species are very like *Pseudococcus* in their cytology—the development of a diploid female-producing parthenogenesis in the female line may well result in the gradual loss of the males from the species, rather than, or before, the assumption of haploidy by them. Similarly in one species of *Icerya*, *Icerya purchasi*, the development of a functional hermaphroditism in the female line, in this case probably subsequent to the establishment of haploidy in the males, seems to be resulting in a marked decrease in the numbers of males in this species, which may well be preparatory to their final complete loss from the species.

*Regulation of the reduction division in
haploids*

If, as we have postulated, the gradual development of male haploidy involves a progressive degeneration on the part of half of the chromosomes and if this degeneration involves first the impairment and then the loss of synapsis, then those species undergoing this evolution must simultaneously acquire a regulative mechanism which will prohibit the random distribution of the normal and the degenerating chromosomes. For it will be recognized that in order to maintain completely functional gametes, the normal chromosomes must be separated from the abnormal in the reduction division. The cytological evidence for such progressive regulation may be presented as follows.

In *Llaveia* the normal mechanism still obtains. Synapsis and pseudoreduction occur and are followed by a reduction division which is perfectly normal in character so far as the chromosomes are concerned. Even in those cases in which the members of one chromosome pair completely fail of synapsis in the primary spermatocyte prophase and go through the first division as independent elements, there occurs a transient attachment of their two derivative chromatids in the prophase of the second division, which is sufficient to ensure the normal reduction of this pair also.

In *Protortonia*, with synapsis almost completely lost, we do indeed find a regulated distribution of chromosomes resulting in a normal reduction, but the mechanism which ensures this result is extremely difficult to analyse. The first division is certainly equational for three, probably for all, of the chromosomes, and the second is positively reductional for the heterochromosome, and probably for all. The five chromatids which enter the second division form short chains,—some-

times two chains of two elements each with the heterochromosome detached, sometimes one chain of two, and one of three elements with the heterochromosome occupying either the terminal or the subterminal position in the latter. The chains then become appressed, bringing the chromosomes into a single row in which only the heterochromosome may be recognized by its size. That its position in the chain, and by analogy the position of the other elements also, is not entirely a matter of chance determination is shown by the following figures. In a total of 358 cells favorable for counting, the heterochromosome was terminal in position in 74 per cent of the cases, subterminal in 23 per cent, and median in 2 per cent, instead of the 2:2:1 ratio to be expected on a purely random placement. Spindle fibers then develop at either end of the single chain of chromosomes and the chain divides transversely, in such a way that three chromosomes always pass to one pole and two to the other. The plane of division is always such as to include the heterochromosome, whatever its position in the chain, in the group of three, never in the group of two, chromosomes. Here then, we are confronted with a successfully regulated reduction without a synapsis of the chromosomes. But what factors underlie the ordered arrangement of the chromosomes which ensures this end is quite unknown.

Pseudococcus, *Phenacoccus*, and *Gossyparia* confront us with a second distinct type of reduction regulation without a preparatory synapsis of the chromosomes. In each of these forms, as remarked above, the abnormal set of chromosomes is regularly separated from the normal set in the second meiotic division. Attempting an analysis of this process, we can discern at least two factors. First, there is a marked tendency for the degenerating het-

eropycnotic chromosomes to stick together in a single mass formation; this mutual adherence may well cause them to act as a single unit and accordingly to pass together to one pole in the reduction division. In the case of *Protortonia*, of course, no such factor can be operative, since there a regulated reductional distribution of the chromosomes is achieved without any trace of such adherence among the chromosomes of either set,—and indeed, it may well be that the clumping of chromosomes in *Gossyparia* and *Pseudococcus* is quite secondary to the regulation of reduction.

The second factor would seem to lie in the spindle mechanism. In the *Pseudococcus-Gossyparia* type the chromosomes of the heteropycnotic group reach their maximum degree of condensation, and are accordingly ready for the division, long before those of the normal group, whose condensation is comparatively slow. A complete half spindle then forms in connection with the chromosomes of the heteropycnotic group, while those of the normal group are still in a relatively diffuse state. The division apparatus being thus complete for the heteropycnotic chromosomes, the division proceeds as far as they are concerned. The normal chromosomes form an inert group not yet ready for division; accordingly no spindle fibers can form in connection with them, and they are simply left behind as the heteropycnotic chromosomes move toward the one pole already formed in the cell. Of course this implies a greater lack of synchrony in the development of the two sets of chromosomes prior to the second or reductional division, than is found in the first division prophase, and cytological proof for this subsidiary hypothesis is not available. Still, since the changes which cause the degeneration of the one chromosome set are primarily changes in

homology with consequent loss of synapsis, a disturbance of the reduction division is perhaps to be expected even though equational mitoses may still go on quite normally. Moreover, strong support for the general idea of the dependence of spindle formation upon chromosome condition is presented by the meiotic divisions of both *Llaveia* and *Protortonia*, for in these cases each separate chromosome, upon reaching a certain definite stage of condensation, forms its own spindle. Further evidence on the same point is offered by certain forms which have already attained the haploid condition. Thus in the primary spermatocytes of certain of the Hymenoptera (in *Paracopidosomopsis*, *Vespa*, and others) a half spindle forms in connection with the single haploid set of chromosomes just prior to the abortive cytoplasmic division. The nuclear division is suppressed entirely in these cases, but there does still occur a slight movement of the single set of chromosomes toward the single pole of the half spindle,—a movement quite comparable to that of the heteropycnotic chromosomes in the *Gossyparia-Pseudococcus* reduction division. In the *Gossyparia-Pseudococcus* cases the presence of the delayed normal group of chromosomes suffices to bring about the completed division of the nucleus. With the final loss of the heteropycnotic group and its precociously formed half spindle, either one of two possibilities might be expected. The reduction division may be omitted entirely. Or, a half spindle may form when the chromosomes of the normal group reach complete condensation, and the division itself be abortive as in the case of the wasps. As a matter of fact, in all the coccids which have become completely haploid in the male sex (*Icerya*, *Crypticerya*, and *Echinicerya*), all trace of a reduction division has been lost. No reduction spindle

forms; a single meiotic division demonstrably equational in character is completed; and normal haploid gametes are thus produced.

It must of course be recognized that whatever factors underlie the regulation of the reduction division in *Protortonia* may also be operative in *Pseudococcus* and *Gossyparia*. Thus the two factors just discussed, the adherence of the chromosomes of one set to each other, and the spindle formation, may, as was suggested earlier, be quite secondary.

All in all, although the cytological data are thus fairly complete, the factors basic to the mechanisms for the regulation of the reduction division warrant no generalization. It will be recalled that in more orthodox cases, the distribution of the members of a pair of chromosomes is assumed to rest on the process of pairing. If such pseudoreduction is requisite to the orderly distribution of a pair of chromosomes to opposite poles, then the elimination of synapsis should lead to irregularities. On this basis it is not clear why, for instance, both members of a pair of chromosomes do not occasionally proceed to the same pole. However, no such irregularities are found in the coccids; whatever the factors which replace pseudoreduction in these cases, they do result in an orderly segregation of the chromosomes. We are not prepared to analyse the relation between pseudoreduction and segregation, ordinarily assumed to be one of cause and effect; we wish only to point out that exceptions to the usual relation are not confined to the coccids. Thus many cases of m chromosomes and XY pairs of sex chromosomes attest the fact that segregation is possible without pseudoreduction. It is not unnatural to assume that in cases such as *Pseudococcus* similar forces controlling the distribution to opposite poles are still active, even though

degenerative changes have otherwise altered one member of each chromosome pair. We are not deluding ourselves in considering that an explanation of the difficulty is thus provided, but we do submit that the question is not confined to the coccids but occurs also in instances far removed from the present ones.

*Induction of parthenogenetic development
in eggs*

The coccids show no transitional stages in the acquisition of this third factor in our tentative analysis of the establishment of a permanent haploidy,—namely, the ability of the mature egg to develop without fertilization. The end stage, in which this ability is already established, is realized in the iceryines. The eggs of these species, whether of a virgin or fertilized female or hermaphrodite, are able to develop without fertilization and with the reduced or haploid chromosome complement. Intermediate stages in the development of such a faculty as this are, to be sure, rather difficult to visualize. One expectation, as suggested before, might take the form of a partial fertilization, in which the sperms only activate the eggs, and take no further part in their subsequent development. However, in *Gossyparia*, in which such a result would appear to be a very natural consequence of the degeneration of the chromosomes in one-half of the spermatids, this condition is not realized. The occasional production of aberrant sperm by the spermatids containing the abnormal chromosomes might seem to justify the suspicion that such a possible partial fertilization might now and again be realized. But the weight of cytological evidence is all against such an hypothesis,—for, in the large number of individuals studied, no actual haploid was ever encountered, nor yet any fertilized egg or embryo prior to the late blastula

stage which contained the set of degenerating chromosomes.

Again, an intermediate condition might be exemplified by a normally diploid species in which some few eggs might occasionally develop independently and without fertilization. No such cases of accidental parthenogenesis have, however, been encountered in the course of the cytological work; nor have breeding experiments, quite extensive in the cases of *Protortonia* and *Pseudococcus*, ever indicated the production of offspring by a virgin female.

Finally, one might expect that, in those species close to haploidy in other respects, as for example in the chromosome conditions in the male line, the eggs would be more than ordinarily susceptible to artificial stimulation and that consequently parthenogenetic development could be induced by experimental means. To test this hypothesis various experiments have been tried with *Pseudococcus* (Schrader, unpublished data). The application of extreme heat and cold during the critical period in the development of the eggs has uniformly failed to induce any parthenogenetic development. Again, the males were X-rayed, in the hope of destroying the chromatin while retaining the ability of the sperm to activate the eggs, and thus inducing gynogenesis,—but always with completely negative results. It should be added, however, that not all the experiments referred to were sufficiently extensive to preclude the possibility of advance along these lines.

So far, then, as our study of the coccids has shown, the ability of the eggs to start development without fertilization or other restoration of diploidy would seem to be of an all or none character. Even those species which we regard as close to haploidy in the male line show no indication of this complementary change in the fe-

male which must of necessity occur if the haploidy is to be permanent. It is possible that the actual achievement of haploidy by the male may somehow induce parthenogenesis in the female, although we must admit that the nature of such a connection is as yet quite inexplicable. That the change in the female is not necessarily induced by the presence of but one kind of sperm, instead of two,—one conceivable way in which haploidy in the male might react upon the female—is shown in *Gossyparia*. That the change has occurred, within the limits of the coccid group, either with or after the establishment of male haploidy, is demonstrated by the iceryines. But we can offer no evidence as to its mode of origin or the nature of its connection, if any, with those changes in the male line which we interpret as indicative of incipient haploidy.

Sex determination

If we adhere to our plan of analysing the problem as a whole by following step by step the conditions presented by the series of coccids here under consideration, this aspect of the subject will also begin with *Llaveia*.

In *Llaveia* the process of sex determination rests on an ordinary XO — XX chromosome mechanism, the male with its five chromosomes representing the heterogametic sex and the female with six chromosomes the homogametic sex. In every way the case seems quite orthodox and there is no reason to suspect that any other than the usual type of sex determination is represented in this species.

The evidence therefore strongly suggests that species with haploid males arose from species in which the ordinary mechanism obtains. *Protortonia* furnishes a very good first departure from the orthodox condition, but it already carries with

it certain stumbling blocks to an analysis. Superficially it is, like *Llaveia*, an instance of XO males and XX females. But if the present interpretation of its meiosis is correct, the chromosomes of the two types of sperm produced are not subject to random segregation. Instead, the X is always associated with two certain autosomes, all three finding homologous partners in the female pronucleus,—whereas the two autosomes in the other type of sperm are never represented in the female at all, being confined strictly to the male line.

But exactly what the bearing of this may be on the next step of the series (*Pseudococcus* and *Phenacoccus*) is not clear, for these animals have apparently lost entirely the sex chromosome mechanism represented in such a typical manner in *Llaveia*. But that a relationship exists between the *Protortonia* and *Pseudococcus* types is more than likely, for the outstanding feature common to both lies in the fact that they have a regulated segregation division through which one half of the autosomes is strictly confined to one type of sperm and the other half to the second type. It is unfortunate that in *Pseudococcus* the tracing of these two groups of chromosomes after the last spermatocyte division to and including the formation of spermatozoa presents some difficulty, for there is some evidence that in *Pseudococcus* the sperms which carry the heteropycnotic group of chromosomes are not always viable. If this proves to be the case, it would bridge the gap to the *Phenacoccus* condition, where the differential mortality in the two types of sperm seems already fully established (unpublished data, Hughes-Schrader).

Be that as it may, the relation that these two groups of chromosomes bear to sex determination is far from clear. It has been suggested independently by Gut-

herz ('23) and Schrader ('23) that one of the groups may represent the X and the other the Y chromosome (their nature perhaps comparable to compound sex chromosomes). It would be difficult to decide which group corresponds to the X and which to the Y, for certainly in ordinary cases the X and Y are not thus differentiated by degrees of heteropycnosis, and there is no reason to ascribe this feature specifically to either X or Y. At any rate, this interpretation does not solve the present difficulty, for two obstacles remain. First, what has occurred to alter the ordinary XO-XX mechanism of the *Llaveia* type to the peculiar conditions of *Pseudococcus* and *Phenacoccus*? And second, what is the mechanism which obtains when one of these two types of sperm fails to become mature or functional? Indeed in *Gossyparia*, where the cytology has been rather fully worked out, the latter condition is completely established, and cytologically speaking, only one of the two groups of chromosomes ever form functional sperm. Moreover, this is not the heteropycnotic group,—for that degenerates and thus demonstrates that if an X-Y chromosome analogy is resorted to, it is the Y that is represented by the precociously condensing chromosomes, and not the X.

The suggestions made in this connection by Schrader ('29) may be mentioned. According to one of these, the unpaired or heterochromosome of *Llaveia* and *Protortonia* males has been eliminated. Indeed, a hint of this may be contained in the behavior of the heterochromosome of *Protortonia*, which, unlike the sex chromosome of *Llaveia*, is lagging instead of precocious in its condensation. Maleness thereafter is the result of a partial or complete incapacitation of one complete set of the autosomes that remain.

This partial or complete incapacitation,

however, has as one of its consequences, the production of one kind of sperm only. Accepting this, as one may well do on the evidence adduced in the *Gossyparia* case, one is confronted with the difficulty of accounting for the production of two sexes with one type of egg and one type of sperm. Manifestly this is not possible under the ordinary conception of the sex chromosome mechanism. Despite the cytological identity of all the sperms produced, two types must be present. It was for this reason that Schrader ('29) suggested that 50 per cent of the sperms carry a gene inducing heteropycnosis in one set of autosomes and that despite cytological evidence to the contrary some crossing over occurs between the chromosomes of the heteropycnotic and those of the normal group. Thus half of the sperms containing the normal group carries the gene while the other half carries its normal allelomorph. (The same is true of the sperms containing the heteropycnotic group, which, however, have no future and need not enter into the final considerations.) Eggs fertilized by sperm carrying the gene for heteropycnosis develop into males—those fertilized by sperm with the normal gene, into females.

But even accepting this highly hypothetical elaboration we are still confronted with the difficulty of a final step. How does the *Gossyparia* stage reach that embodied in the iceryine coccids, where haploidy is actually established? Here the explanation no longer rests solely on the sperms, for the egg unaided produces males, while all fertilized eggs give rise to females only.

The promise of a different attack always inherent in the investigation of exceptional cases is given by the discoveries of A. R. and P. W. Whiting (Whiting, P. W. & Whiting, A. R., '25; Whiting, A. R., '27a, '27b) in *Habrobracon*. In exceptional cases there are produced here males which show not only mater-

nal but also paternal characters. They therefore have come from fertilized eggs. Moreover the genetic evidence, although concededly not entirely conclusive, strongly suggests that at least some of these males are diploid. The high degree of sterility in these males suggests abnormality, but that fact by no means rules out the possibility that an elucidation of the conditions in these very males may throw much light on the processes involved in haploid parthenogenesis.

We can do no more than suggest as we have done earlier that at present only two hypotheses will take all the known facts into account.

One is that of Goldschmidt, which assumes that maleness is carried in the cytoplasm of the egg and is constant, while femaleness is carried in the chromosomes. If $FF > M > F$, then the presence of one set of chromosomes (as in the unfertilized egg) or two sets of chromosomes (as in the fertilized egg) will determine the sex of the developing individual. We repeat that this hypothesis should be kept in mind in all future consideration of the question. A demonstration of its correctness would imply that in the interval between the conditions in *Gossyparia* and those of *Icerya*, the main change consisted in the acquisition of the faculty of imposing the factor for maleness on the cytoplasm of the egg.

The second hypothesis is the algebraic sum hypothesis of Schrader and Sturtevant already mentioned earlier in the paper. Its departure from Bridges' interpretation lies primarily in the conception of the action of the sex determining factors. According to Bridges, sexual or any other characters are the index of a point of balance of genes concerned in their expression. As long as the proportion of the number of X chromosomes to the sets of autosomes is the same this genic balance will not be altered, and thus $X + A = 2X + 2A = 3X + 3A = 4X + 4A = \text{female}$.

On the hypothesis of Schrader and Sturtevant the decision rests on the degree of preponderance of the genetic effect of the factors for one sex over those of the other sex. A certain degree of such preponderance is necessary before a clearcut determination of sex is possible. Thus it was suggested that on the basis of arbitrarily assigning appropriate numerical values to the X chromosome (or femaleness) and to the autosomes (or maleness), a difference of five or less brings about male development, whereas a difference of seven or greater is conducive to female development (see Table I). It will be recognized that if the X has one value and A another, the difference between them will increase as the haploid sets of chromosomes increase in number, and that thus a range from maleness to femaleness will result.

Although very close to his own general interpretation, this hypothesis is not accepted by Goldschmidt ('27, page 675). Bridges' objections, as already stated, are based mainly on the fact that the numerical differences between diploid and triploid individuals on the one hand and males and females on the other are disproportionate to the phenotypical differences actually observed,—and furthermore that his evidence in certain mosaics of *Drosophila* indicates that haploid individuals of that species would indeed be female if viable. The evidence for the latter claim is, however, incomplete; and while the former seems admittedly well founded, we submit that in view of our lack of knowledge of the reactions involved no final decision is warranted. Withal it is of course possible, as Bridges himself suggests ('25), that cases such as *Icerya* cannot be placed upon the same basis as *Drosophila*.

There can be little doubt that the genic balance hypothesis is supported by a great body of evidence and that in general poly-

loidy does seem to induce no phenotypic changes other than those inherent in the different cell sizes involved. On the other hand, polyploid forms have never been subjected to a complete analysis from this point of view. Thus even von Wettstein ('24), whose conclusions on this point agree with those of Bridges, mentions the fact that in one of the mosses, *Bryum caespiticum*, the experimentally produced hermaphroditic tetraploid gametophyte showed a markedly increased protandry when compared with the diploid gametophyte of the same species. Not only were the male organs older when the female organs developed, but the proportion of female to male organs was altered from 1 ♀ to 4.98 ♂ in the diploid gametophyte to 1 ♀ to 13.3 ♂ in the tetraploid. These changes are certainly not interpretable on the basis of cell size differences alone.

Again, Blakeslee and Belling ('24) state that in the shape of the capsules of diploid and tetraploid *Datura* plants "we seem to have a qualitative rather than a quantitative change of form."

Finally may be mentioned the recent findings of Mangelsdorf and Fraps ('31), who report that in *Zea mays* a definite quantitative relationship exists between the number of genes for yellow pigmentation (Y) and the amount of vitamin A produced in the endosperm. The presence of the allelomorph gene y induces the production of only a negligible quantity of this enzyme (less than .05 units per gram) whereas in the presence of one Y this quantity rises to 2.25 units per gram. However, the most striking feature so far as the present discussion is concerned lies in the fact that the number of Y genes has a direct and progressive effect on this quantity, so that 2 Y bring about the production of 5 units, and 3 Y the production of 7.5 units per gram,—the triple dose being made possible of course by the fact that

the endosperm is triploid. If now an experiment could be devised to decide whether a varying number of haploid sets (each carrying Y) produces correspondingly varying amounts of enzyme, the two hypotheses in question could be tested. Such an experiment would become possible if a tetraploid (or any polyploid higher than triploid) endosperm could be obtained, as for instance by the use of X rays or the effect of temperature changes.

The fate of the algebraic sum hypothesis thus may be finally decided if such work as that of Mangelsdorf and Fraps be pushed further in the direction indicated. So far as the hypothesis of Goldschmidt is concerned it may be pointed out that it already has received support in his own findings on *Lymantria*. For if, as he believes, certain factors in the Y exert an effect on the future sex determination before the egg has been fertilized such an influence must occur through the cytoplasm.

LIST OF LITERATURE

- ANKEL, W. E. '27. Neuere Arbeiten zur Zytologie der natürlichen Parthenogenese der Tiere. Zeitsch. f. ind. Ab. u. Vererb., 45.
- . '29. Neuere Arbeiten zur Zytologie der natürlichen Parthenogenese der Tiere (Fortsetzung). Zeitsch. f. ind. Ab. u. Vererb., 52.
- ARMBRUSTER, L. '13. Chromosomenverhältnisse bei der Spermatogenese solitärer Apiden (*Osmia cornuta* Latr.). Beiträge zur Geschlechtsbestimmungsfrage und zum Reduktionsproblem. Arch. f. Zellforsch., 11.
- BEADLE, G. W., and MCCLINTOCK, B. '28. A genic disturbance of meiosis in *Zea mays*. Science, 68.
- BEADLE, G. W. '30. Genetical and cytological studies of mendelian asynapsis in *Zea mays*. Memoir 129 Cornell Univ. Agric. Exp. Sta.
- BELLING, J., and BLAKESLEE, A. F. '23. The reduction division in haploid, diploid, triploid, and tetraploid *Daturas*. Proc. Nat. Ac. Sci. Wash., 9.
- . '27. The assortment of chromosomes in haploid *Daturas*. La Cellule, 37.
- BLAKESLEE, A. F., and BELLING, J. '24. Chromosomal mutations in the Jimson weed, *Datura stramonium*. Jour. Hered., 15.
- BRIDGES, C. B. '25a. Sex in relation to chromosomes and genes. Am. Nat., 59.
- . '25b. Haploidy in *Drosophila melanogaster*. Proc. Nat. Acad. Sci., 11.
- . '30. Haploid *Drosophila* and the theory of genic balance. Science, 72.
- BUTTEL-REEPENS, H. v. '04. Über den gegenwärtigen Stand der Kenntnisse von den geschlechtsbestimmenden Ursachen bei der Honigbiene (*Apis mellifica* L.), ein Beitrag zur Lehre von der geschlechtlichen Präformation. Verh. deutsch. Zool. Ges., 14.
- CASTLE, W. E. '30. The quantitative theory of sex and the genetic character of haploid males. Proc. Nat. Acad. Sci., 16.
- CHIPMAN, R. H., and GOODSPEED, T. H. '27. Inheritance in *Nicotiana tabacum*: VIII. Cytological features of purpurea haploid. Univ. Calif. Pub. Bot., 11.
- CLAUSEN, R. E., and MANN, M. C. '24. Inheritance in *Nicotiana tabacum*: V. The occurrence of haploid plants in interspecific crosses. Proc. Nat. Acad. Sci., 10.
- DAVIS, B. M., and KULKARNI, C. G. '30. Cytology and genetics of a haploid sport from *Oenothera franciscana*. Gen., 15.
- DONCASTER, L. '06a. On the maturation of the unfertilized egg and the fate of the polar bodies in the Tenthredinidae (Sawflies). Q. J. M. S., 49.
- . '06b. Spermatogenesis in the honey bee (*Apis mellifica*). Anat. Anzeig., 29.
- . '07a. Spermatogenesis in the honey bee. Anat. Anzeig., 31.
- . '07b. Gametogenesis and fertilization in *Nematus ribesii*. Q. J. M. S., 51.
- . '09. Gametogenesis of the sawfly, *Nematus ribesii*—a correction. Nature.
- . '10. Gametogenesis of the gall-fly, *Neuroterus lenticularis*. Part I. Biol. Proc. Roy. Soc., 82.
- . '11. Gametogenesis of the gall-fly, *Neuroterus lenticularis*. Part II. Biol. Proc. Roy. Soc., 83.
- . '16. Gametogenesis and sex determination in the gall-fly, *Neuroterus lenticularis*. Part III. Biol. Proc. Roy. Soc., 89.
- DONCASTER, L., and CANNON, H. G. '20. On the spermatogenesis of the louse (*Pediculus corporis*

- and *P. capitis*) with some observations on the maturation of the egg. *Quart. Jour. Mic. Sci.*, 64.
- EMERSON, S. H. '29. The reduction division in a haploid *Oenothera*. *La Cellule*, 39.
- GAINES, E. F., and AASE, H. C. '26. A haploid wheat plant. *Amer. Jour. Bot.*, 13.
- GATES, R. R., and GOODWIN, K. M. '30. A new haploid *Oenothera*, with some considerations on haploidy in plants and animals. *Jour. Gen.* 23.
- GODLEWSKI, E. '13. *Physiologie der Zeugung*. In Winterstein, H. *Handbuch der vergleichenden Physiologie*. 3. Jena.
- GOLDSCHMIDT, R. '20. *Mechanismus und Physiologie der Geschlechtsbestimmung*. Gebr. Borntraeger, Berlin.
- . '27. Die zygotischen sexuellen Zwischenstufen und die Theorie der Geschlechtsbestimmung. *Ergeb. der Biol.*, 2.
- GRANATA, L. '09. Le divisioni degli spermatociti di *Xylocopa violacea* L. *Biologica*, 2. Torino.
- . '13. Ancora sulle divisioni degli spermatociti di *Xylocopa violacea* L. *Monit. Zool. Ital.*, 24.
- HERTWIG, P. '20. Haploide und diploide Parthenogenese. *Biol. Zentralbl.*, 40.
- HERTWIG, R. '05. Über das Problem der sexuellen Differenzierung. *Verh. deutsch. Zool. Ges.*, 16.
- . '07. Weitere Untersuchungen über das Sexualitätsproblem. *Verh. deutsch. Zool. Ges.*, 17.
- HOUASSE, R. '22. La régulation du nombre des chromosomes chez les embryons parthénogénétiques de grenouille rousse. *Comp. Rend. Acad. Sci. Paris*, 174.
- HUGHES-SCHRADER, S. '25. Cytology of hermaphroditism in *Icerya purchasi* (Coccidae). *Zeit. f. Zellf. u. mik. Anat.*, 2.
- . '26. Spermatogenesis in *Icerya purchasi*—a correction. *Science*, 63.
- . '27. Origin and differentiation of the male and female germ cells in the hermaphrodite of *Icerya purchasi*. *Zeit. f. Zellf. u. mik. Anat.*, 6.
- . '30. The cytology of several species of iceryine coccids with special reference to parthenogenesis and haploidy. *Jour. Morph. and Phys.*, 50.
- . '31. A study of the chromosome cycle and the meiotic division-figure in *Llaveia bouvari*—a primitive coccid. *Zeit. f. Zellf. u. mik. Anat.* 13.
- JØRGENSEN, C. A. '28. The experimental formation of heteroploid plants in the genus *Solanum*. *Jour. Gen.*, 19.
- LAMS, H. '08. Les divisions des spermatocytes chez les Fourmi. (*Camponotus herculeanus* L.) *Arch. f. Zellf.*, 1.
- LENHOSSÉK, M. v. '03. Das Problem der geschlechtsbestimmenden Ursachen. Jena.
- LENSEN. '98. Contribution à l'étude du développement et de la maturation des œufs chez l'*Hydatina senta*. *Zool. Anzeig.*, 21.
- MANGELSDORF, P. C., and FRAPS, G. S. '31. A direct quantitative relationship between vitamin A in corn and the number of genes for yellow pigmentation. *Science*, 73.
- MARK, E. L., and COPELAND, M. '06. Some stages in the spermatogenesis of the honey bee. *Proc. Am. Acad. Arts. and Sci.*, 42.
- . '07. Maturation stages in the spermatogenesis of *Vespa maculata* L. *Proc. Am. Acad. Arts and Sci.*, 43.
- MEVES, F. '04. Über "Richtungskörperbildung" im Hoden von Hymenopteren. *Anat. Anzeig.*, 24.
- . '07. Die Spermatocyten bei der Honigbiene (*Apis mellifica* L.) nebst Bemerkungen über Chromatinreduktion. *Arch. mik. Anat.*, 70.
- MEVES, F., and DUESBERG, J. '08. Die Spermatocytenteilungen bei der Hornisse (*Vespa crabro* L.). *Arch. mik. Anat.*, 71.
- NACHTSHEIM, H. '13. Cytologische Studien über die Geschlechtsbestimmung bei der Honigbiene (*Apis mellifica* L.). *Arch. f. Zellf.*, 11.
- . '21. Sind haploide Organismen lebensfähig? *Biol. Zent.*, 41.
- OEHNINGER, M. '13. Über Kerngrößen bei Bienen. *Verh. d. Phys.-Med. Ges. zu Würzburg, N. F.*, 42.
- PATTERSON, J. T. '17a. Studies on the biology of *Paracopidosomopsis* I. Data on the sexes. *Bio. Bul.*, 32.
- . '17b. Studies on the biology of *Paracopidosomopsis* III. Maturation and fertilization. *Bio. Bul.*, 33.
- . '21. The development of *Paracopidosomopsis*. *Jour. Morph.*, 36.
- . '28a. Functionless males in two species of *Neuroterus*. *Bio. Bul.*, 54.
- . '28b. Sexes in the *Cynipidae*, and male-producing and female-producing lines. *Bio. Bul.*, 54.
- PATTERSON, J. T., and HAMLETT, G. W. D. '25. Haploid males in *Paracopidosomopsis*. *Science*, 61.
- PATTERSON, J. T., and PORTER, L. T. '17. Studies on the biology of *Paracopidosomopsis* II. Spermatogenesis of males reared from unfertilized eggs. *Bio. Bul.*, 33.

- PARMENTER, C. L. '20. The chromosomes of parthenogenetic frogs. *Jour. Gen. Phys.*, 2.
- . '25. The chromosomes of parthenogenetic frogs and tadpoles. *Jour. Gen. Phys.*, 8.
- . '26. The chromosomes of parthenogenetically developed young tadpoles and early cleavages of *Rana pipiens*. *Anat. Rec.*, 34. (Abstract No. 97.)
- PEACOCK, A. D. '25. Haploidy in the male saw fly (Tenthredinidae) and some considerations arising therefrom. *Nature*, 116.
- PEACOCK, A. D., and SANDERSON, A. R., '31. Cytological evidence of male haploidy and female diploidy in a saw fly (Hymen. Tenthred.) *Proc. 2nd Internat. Cong. Sex Research*.
- PETRUNKEWITSCH, A. '01. Die Richtungskörper und ihr Schicksal im befruchteten und unbefruchteten Bienenerei. *Zool. Jahrb., Abt. Anat.*, 14.
- PIERANTONI, U. '10. La simbiosi ereditaria e la biologia sessuale d'*Icerya*. *Monit. Zool. Ital.*, 21.
- . '12. Studio sullo sviluppo d'*Icerya purchasi* Mask. Parte I. Origine ed evoluzione degli elementi sessuale femminili. *Arch. Zool. Ital.*, 5.
- . '14a. Studio sullo sviluppo d'*Icerya purchasi* Mask. Parte II. Origine ed evoluzione degli elementi sessuale maschili.—Ermafroditismo. *Arch. Zool. Ital.*, 7.
- . '14b. Studio sullo sviluppo d'*Icerya purchasi* Mask. Parte III. Osservazioni di embriologia. *Arch. Zool. Ital.*, 7.
- SCHRADER, F. '20. Sex determination in the white fly (*Trialeurodes vaporariorum*). *Jour. Morph.*, 34.
- . '21. The chromosomes of *Pseudococcus nipae*. *Bio. Bul.*, 40.
- . '23a. A study of the chromosomes in three species of *Pseudococcus*. *Arch. f. Zellf.*, 17.
- . '23b. Sex ratio and oogenesis of *Pseudococcus citri*. *Zeit. f. ind. Ab. u. Verer.*, 30.
- . '23c. Haploidie bei einer Spinnmilbe. *Arch. f. mik. Anat.*, 97.
- . '23d. Origin of mycetocytes in *Pseudococcus*. *Bio. Bul.*, 45.
- . '29. Experimental and cytological investigations of the life-cycle of *Gossyparia spuria* (Coccidae) and their bearing on the problem of haploidy in males. *Zeit. f. wiss. Zool.*, 134.
- . '31. The chromosome cycle of *Protortonia primitiva* (Coccidae) and a consideration of the meiotic division apparatus in the male. *Zeit. f. wiss. Zool.*, 138.
- SCHRADER, F., and HUGHES-SCHRADER, S. '26. Haploidy in *Icerya purchasi*. *Zeit. f. wiss. Zool.*, 128.
- SCHRADER, F., and STURTEVANT, A. H. '23. A note on the theory of sex determination. *Am. Nat.*, 57.
- SHULL, A. F. '21. Chromosomes and the life cycle of *Hydatina senta*. *Bio. Bul.*, 41.
- STORCH, O. '24. Die Eizellen der heterogonen Rädertiere. Nebst allgemeinen Erörterungen über die Cytologie des Sexualvorganges und der Parthenogenese. *Zool. Jahrb., Abt. Anat.*, 45.
- TAUSON, A. '24. Die Reifungsprozesse der parthenogenetischen Eier von *Asplanchna intermedia* Huds. *Zeit. f. wiss. Biol.*, 1.
- . '27. Die Spermatogenese bei *Asplanchna intermedia* Huds. *Zeit. f. Zellf. u. mik. Anat.*, 4.
- THOMSEN, M. '27. Studien über die Parthenogenese bei einigen Cocciden und Aleyrodiden. *Zeit. f. Zellf. u. mik. Anat.*, 5.
- WETTSTEIN, F. v. '23. Kreuzungsversuchen mit multiploiden Moosrasen. *Bio. Zentralbl.*, 43.
- WHITING, A. R. '27a. Genetic evidence for diploid males in *Habrobracon*. *Bio. Bul.*, 53.
- . '27b. Genetic evidence for diploid males in *Habrobracon*. *Am. Nat.*, 62.
- WHITING, P. W. '18. Sex determination and biology of a parasitic wasp, *Habrobracon brevicornis* (Wesmael). *Bio. Bul.*, 34.
- WHITING, P. W., and WHITING, A. R. '25. Diploid males from fertilized eggs in Hymenoptera. *Science*, 62.
- WHITNEY, D. D. '09. Observations on the maturation stages of the parthenogenetic and sexual eggs of *Hydatina senta*. *Jour. Exp. Zool.*, 6.
- . '24. The chromosome cycle in the rotifer *Asplanchna intermedia*. *Anat. Rec.*, 29.
- . '29. The chromosome cycle in the rotifer *Asplanchna amphora*. *Jour. Morph. and Phys.*, 47.
- WIEMAN, H. L. '15. Observations on the spermatogenesis of the gall-fly, *Dryophanta erinacei* (Mayr.). *Bio. Bul.*, 28.
- WIGGENHORN, B., and WHITNEY, D. D. '25. The individuality of the germ nuclei during the cleavage of the fertilized egg of the rotifer *Asplanchna intermedia*. *Bio. Bul.*, 48.
- WILSON, E. B. '09. Recent researches on the determination and heredity of sex. *Science*, 29.
- WITSCHI, E. '29. Bestimmung und Vererbung des Geschlechts bei Tieren. *Handb. der Vererbungswiss.*, 2.
- VANDEL, A. '31. La Parthénogenèse. Paris.



HIBERNATION IN MAMMALS

By GEORGE E. JOHNSON

Kansas State Agricultural College

(Contribution 133 from the Department of Zoology, Kansas State Agricultural Experiment Station, Manhattan, Kansas)

HIBERNATION is often referred to as "winter-sleep" in English, "*Winterschlaf*" in German and "*sommeil-hivernal*" in French. It is also called "torpor," "lethargy," and, in Italian, "*letargo*." These terms may be considered essentially synonymous. They involve an inactive state in which the metabolism is so greatly lowered that the body temperature is only a little higher than that of the surroundings. A limitation of the term hibernation to this condition and not applying it in the older more literary sense of "spending the winter" would make the meaning of the word clearer.

It should be stressed that hibernation is not ordinary sleep occurring in the winter. This was recognized long ago by Horvath (1881), who repeated a statement of the botanist, Ferd. Cohn, that "*Winterschlaf*" is not sleep and has nothing to do with winter. In this way he emphasized that hibernation may occur even in the summer and that the insensibility is far deeper than in ordinary sleep. If such a meaning can be given "*Winterschlaf*" there should be little difficulty in limiting the term "hibernation" to actual states of torpor and also in having it include all such states, not excepting those that occur in summer in the field or laboratory. There is no evidence that mammals ever become insensitive or partly torpid because of warm surroundings, all reported

cases of lowered metabolism apparently having occurred when the surrounding temperature was considerably below that of the normal animal. For this reason the term "aestivation" appears inappropriate for summer torpor in mammals, although it may be proper for inactivity actually produced by surrounding high temperatures. Aestivation might be used for the denning up of the animals following a drying of the vegetation by the heat in the summer, but since any known cases of semi-torpor at this season are produced by cold such conditions should, it would seem, be called partial hibernation.

ANIMALS THAT HIBERNATE

Hibernation is common in such invertebrates as the snails in the Mollusca and the crustaceans, insects, arachnids and myriapods in the Arthropoda. It is the usual winter condition of most amphibians in colder climates and of terrestrial reptiles such as the tortoises, lizards and snakes. Invertebrates and the lower vertebrates are generally considered as having no heat-regulating mechanism, and since their temperature varies chiefly with that of the surroundings they are said to be poikilothermal or cold blooded. Recently, however, evidence has been produced that the turtle has some power to regulate the temperature of its body (Baldwin, 1925). All birds and most mammals maintain a relatively high and almost con-

stant body temperature regardless of the environment, and are said to be homoiothermal or warm blooded. Hibernating mammals do not appear to maintain a very constant temperature and at times definitely assume the poikilothermal state, so that their temperature is only a little higher than that of the surrounding atmosphere or soil.

Hibernation has been studied by various workers in monotremes, insectivores (hedgehogs), bats, and in several genera of rodents (woodchucks, dormice, ground squirrels, prairie dogs, some chipmunks and certain jumping and pocket mice). Mills (1892) says the porcupine, a large spiny rodent, hibernates but Pratt (1923) and Anthony (1928) state that this animal does not hibernate. According to Pratt (1923) and Bailey (1926) some northern species of carnivores (raccoons, skunks and badgers) hibernate. Anthony (1928) states that raccoons hibernate and skunks and badgers "den up" during very cold weather. All three of these writers state that some bears hibernate. Other workers (e.g. Merzbacher, 1904) deny that bears enter into a real state of hibernation and call attention to the fact that the young, usually two in number, are born in late winter and that the body temperature of the mother could not be low at that time. Dubois (1896) calls attention to the vapors emerging from the winter den of the bear, and he and Adler (1926) each state that bears and badgers maintain a high temperature. Seron (1928) states that the raccoon, skunk and bear are partial hibernators in the northern regions, but that they do not assume a death-like torpor.

It may be noted that the hibernating animals do not belong to any one order but that most of them live in the ground and have no access to their usual food during the time the ground is frozen. Horvath (1874, 1881) sought some test whereby one could determine whether a given species could hibernate or not. He found that animals that were known not to hibernate would die when immersed to the neck in cold water if the body temperature fell below 19°C. (essentially confirmed by Britton, 1922), whereas known hibernators would survive at body temperatures a few degrees above the freez-

ing point of water. The latter finding was confirmed by Tait and Britton (1923), who found that a woodchuck would recover if its body was cooled even to 3°C. by the immersion method. The author has observed that ground squirrels, caught by "drowning out" methods become very torpid while wet in cold air, but recover when warmed. It seems probable that this test developed by Horvath may help in distinguishing between hibernators and non-hibernators. However, placing several animals of a species in a cold environment in the fall and winter probably would be the safer practice.

PLACE OF HIBERNATION

Barkow (1846) states that bats hibernate in stone walls, cellars, and hollow trees. Dormice hibernate in dry holes under rocks, roots or garden walls, depending on the species, and the hedgehog hibernates under roots of trees and shrubs and under garden walls. He also states that the hamster hibernates 5-10 feet and the marmot 3-7 feet underground in a nest lined with vegetation and that it closes its burrow in the winter. North American bats hibernate largely in caves (Bailey, 1924; Hahn, 1908). Ground squirrels hibernate in nests made of dry vegetation in hollowed-out underground chambers connected with their burrows. The chambers vary as to depth and size with the species. In the thirteen-lined ground squirrel, with which the author has worked, 24 nests studied varied from 4 to 10 inches in diameter and from about 3 to 27 inches below the surface (Johnson, 1917). In this and other species these nests may be connected with a drain and the entrance to the burrow is always plugged with soil before hibernation (Johnson, 1917; Shaw, 1925a). Prairie dogs hibernate in larger nests 10 or more feet below the surface (Merriam, 1901; Swenk, 1915). Their nests may be above the main tunnel as a protection against the burrow being filled with water; the entrance is not closed, possibly because the animals hibernate less than ground squirrels. Other American rodents hibernate under ground or in nests under stones. Apparently raccoons hibernate in hollow logs. If skunks and badgers hibernate they would do so in underground chambers where they normally sleep.

Food stores are sometimes found in the nests of rodents. An unusual case was observed by the author. A ground squirrel, *Citellus tridecemlineatus tridecemlineatus*, had stored about 24,000 kernels of oats

in one underground chamber and about 4,000 in another (Johnson, 1917). Oats, wheat, corn and weed seeds were frequently found in the excavations in which the hibernation nests were made, but in decreasing quantities with the advance of autumn (Johnson, 1917), suggesting that this food is eaten chiefly before entrance into hibernation. However, storage of grain was not found to be universal in this species (Johnson, 1917; Fitzpatrick, 1925). Bailey (1926) reports that there is storage of seeds and grains in the pocket mice and some of the chipmunks which are not very fat when they hibernate but apparently wake at intervals to eat.

Whether animals store food or not probably depends partly on its abundance preceding the hibernation period. While different species do not hibernate at the same time or become equally torpid, it is generally agreed by most writers that hibernation serves to conserve the life of the species that hibernate and that torpor is associated primarily with a cold season when food is impossible to secure. Whether every such species would perish if it should not be able to become torpid is difficult to determine, but this appears probable.

HIBERNATION IN THE SUMMER

That hibernation is not a condition which can occur only in the winter has been shown by a number of workers. Forel (1887) found that two dormice hibernated first in the spring after becoming fat and remained lethargic most of the summer. Horvath (1881) observed hibernation in ground squirrels in the laboratory at 22°C. Polimanti (1912) refers to summer torpor observed by Brown-Sequard in dormice lasting a week at external temperatures of 15° to 20°C., and also in marmots (European woodchucks) in June at external temperatures of 21.5° to 23°C. Bats may hibernate in June at 15°–16°C. according to Koennick (Adler, 1926). Summer torpor in thirteen-lined ground squirrels has been observed by the author to take place in a refrigerator each summer since 1924 (Johnson, 1925, 1930). In fact, hibernation was found more commonly in the summer than in the spring (Johnson, 1930). Many cases of partial hibernation have been observed in the animal house on cool mornings in August and also during later fall and winter months when the temperature fell to about 21°C. With what may be considered typical summer temperatures of about 24°C. or above no hibernation

was observed. Cases of partial hibernation on cool summer days have been reported in the Townsend ground squirrel by Shaw (1925b) and in the thirteen-lined form by Wade (1930).

The tenrec of Madagascar has often been cited as an animal that hibernates in summer, but Milne-Edwards (1857) has pointed out that several workers have reported this animal hibernating during the cold season.

Since hibernation may occur in the summer in the laboratory it would be expected that it may also occur in the field, as Horvath (1881) suggested, at temperatures below 22°C. A "drowsy" Columbian ground squirrel was dug out of its burrow in August, but all efforts to find a torpid animal prior to December 13 failed (Shaw, 1925a). Seeking for this condition in the thirteen-lined ground squirrel Wade (1930) procured his earliest record of hibernation on October 16. If the animals are partly torpid in the early fall, they must be so slightly torpid that they are aroused by the sounds of the digging and are fully active when found.

Indirect evidence that such a condition may occur in nature is produced by Shaw (1925a), who found that the Columbian ground squirrels had almost all retired to their burrows by August 10 one year and in another drier summer all had disappeared by August 7 (1925c). Similar observations that hot dry weather and a consequent drying of vegetation send ground squirrels (related to our prairie dogs) of Turkestan into their burrows by June 1 is given by Kashkarov and Lein (1927). Wade (1930) mentions the disappearance of wild thirteen-lined ground squirrels one year in eastern Nebraska in hot weather early in September. He also found that of 22 animals transferred to outdoor pens in the spring nine plugged the entrance to their burrows, one in May, two in July, five in August and one in September. Wade also states that the individuals at large in the fields in late September were young or lean ones.

It has been the experience of the author that it is more difficult to secure ground squirrels from boys in western Kansas in August and September than in April to July, a fact which would support Wade's statement. However, many animals have been secured in the fall in the Dakotas, in Illinois and in Kansas, even as late as September and October.

LENGTH OF HIBERNATION

Two things make it difficult to state how long a given species hibernates. One of these is the apparent tendency of torpid mammals to wake up at intervals and the other is the possibility of some individuals of a species hibernating in the early fall when others are still at large. The waking of hibernating

mammals every few days has been observed by Barkow (1846) in ziesels or ground squirrels after one to seven days of torpor, and in hedgehogs; by Horvath (1878) in ground squirrels after torpor for four days; by Mangili (1807), Valentin (1857) and Dubois (1896) in marmots, after periods of torpor varying from a few days to three or four weeks; and by Shaw (1925a, b) in the Columbian and Townsend ground squirrels.

The author has found in many experiments, each involving 20 animals kept in the refrigerator for two weeks, that some of the animals will usually hibernate within one to three days and then awakened from one to ten days later, remaining active for a day or more. In cases where animals were in the refrigerator for long periods, castrated males were in continuous hibernation as long as 15, 16, 18 and 33 days and normal males for 13, 14 and 15 days, as judged by daily observations and their lack of feeding.

To avoid any possibility of animals waking between daily observations unbeknown to the observer, further records were taken for over four months on eight *C. r. pallidus* ground squirrels which had already been in the refrigerator 25 days. Three or four grains of oats were dropped gently on the back of the torpid animal, which would fall off only when the animal woke or moved about. The food placed in the cages consisted of dry oats and a small amount of green grass at first, but later carrots and a few kernels of oats were placed in the cages. The animals were seldom handled as previous observations had confirmed Dubois' (1896) statement that taking temperatures, etc., caused more frequent awakening. The grains of oats appeared not to stimulate waking. The range of continuous hibernation was from one to eighteen days with an average of approximately six days. One record each of 18, 17, 14 and 13 days of continuous hibernation was made, but four records of 11 days and six records of 10 days were made. There appeared to be some tendency towards a lengthening of the periods of hibernation from an average of about four at first to about eight days after a few weeks in the refrigerator. This may indicate that the torpor is more prolonged after the first few periods, although it is probably partly accounted for by the lowering of the refrigerator temperature from about 11° to about 3°C. during the course of the experiment. The average time during which the animals remained awake between periods of torpor was approximately one day. The faeces voided by each animal during the first two months of this experiment were proportional to the time spent awake. On the 62nd day of the experiment the animals were carefully transferred to clean cages and in a total of over 80 observations the animals, almost without exception, were found to void an appreciable amount of

urine and faeces each time they were awake. In some cases as many as 20 or 25 faecal masses and large amounts of urine were seen. Apparently when such surprising amounts were found the animal had eaten more freely than usual. It appeared probable that most of the food passed through the animal before it became torpid again. These observations support the statements of others that these short periods of waking are caused by the stimuli produced by the urine in the bladder and faeces in the rectum.

Carrots and apples fed at different times in the experiment usually showed tooth marks after an animal had been awake for a few hours, but in several instances no food appeared to have been eaten. A few grains of oats were sometimes hulled and eaten, but most of the oats were left untouched. While the quantities of food taken at any one time were as a rule small, it should be stated that near the end of the experiment and to a less extent at other times an animal which was thin might consume large quantities of carrots in one or two days and then go back into hibernation. In general, these observations confirm those of Horvath (1878), who found that ground squirrels ate when awake more than a few hours.

It is not known whether animals wake at intervals in their burrows. One of the author's animals, which had built its nest within six inches of the surface in an outdoor cage in Chicago, came out of its burrow in late December and in late January when the weather was warm. It seems quite probable that waking occurs at intervals throughout the winter in nature, for the ground squirrels continued to do so in the refrigerator even at 2°-3°C. Waking may be more frequent in the fall because at that time the soil temperature and therefore the metabolism is higher than in mid-winter and there will be formed more urine and faeces.

Different individuals of a single species may not spend the same amount of time in hibernation. Old hedgehogs may hibernate earlier than young ones (Barkow, 1846). Old ground squirrels den up first and the females go in before the males and appear several days later in the spring (Shaw, 1925b; Wade, 1930; Johnson, unpublished data), so that the average period spent underground by the Columbian ground squirrel is 220 days in the female and 204 days in the male (Shaw, 1925b). The fact that these animals are doubtless not torpid all of this time, together with the other variations also presented, will make it clear that only approximate figures can be given for the length of hibernation in different species.

According to Barkow (1846) the hedgehog is underground four to five months, from November or December to March or April. Merzbacher (1904) gives this period as three or four months for the

hedgehog and Lapland marmot, and two or three months for German marmots, badgers, dormice and ground squirrels. Howell (1915) states that woodchucks hibernate four to six months. Raccoons hibernate nearly four months in the Red River Valley (Seton, 1928) and three to four months in Ohio (Williams, 1909). Thirteen-lined ground squirrels have been seen as late as October in Illinois (Corey, 1912; Johnson, 1917), in South Dakota (Hahn, 1914; Johnson, 1917) and in Nebraska (Wade, 1930), and on November 9 in Colorado (Burnett, 1914). They appear again in March, sometimes early (Hahn, 1914, in South Dakota) but more often late in the month (Burnett, 1914, Colorado; Corey, 1912, Illinois). In Kansas both the typical variety and the paler variety from the western part have generally been procured in fairly good numbers late in March.

POSITION IN HIBERNATION

In hibernation rodents are rolled up in their nests in the ordinary sleeping position. Striped ground squirrels sit on the posterior surface of the hind legs, the back strongly arched above, the nose tucked into the fur of the posterior part of the abdomen so that the top of the head rests partly against the pelvic girdle and partly on the bottom of the nest. The weight of the animal appears to be divided between the hind legs, the posterior dorsal part of the sacrum and the posterior dorsal part of the head. The Townsend species is illustrated in this position by Shaw (1925b), but the Columbian rests on the sacrum alone (Shaw, 1925a) as does also the *Callospermophilus* form. The fore legs are held close at the sides of the head. The eyes and mouth are tightly closed. The outside curvature of the body describes nearly a circle and it lacks only a little width in the middle to form a perfect sphere. This position doubtless tends to conserve body heat.

IMPERFECT TEMPERATURE CONTROL OF HIBERNATING MAMMALS

That the temperature of hibernating mammals, even when not torpid, may be lower than in mammals which do not hibernate was observed long ago by Saissy (1815) and others. Saissy gave records of 25°–30°R. (32.2°–37.5°C.) for woodchucks, hedgehogs, dormice and bats. Barkow (1846) observed a drop in temperature in hedgehogs and bats in ordinary sleep, in sickness and in starvation, but concluded that they are ordinarily warm blooded when awake, bats even having temperatures as high as 41.0° and 41.6°C. Dubois (1896) also found no fluctuation in the temperatures of hibernators except in the fall. According to Merzbacher (1904), Hall found a drop in

temperature in a bat during its day sleep. Marked fluctuations in temperature in *Citellus tridecemlineatus* and also in *C. t. pallidus* have been observed at all times of the year (Johnson, 1928). The temperatures of ground squirrels when not in hibernation ranged from about 32° to about 41°C., but a range of 35° to 39°C. was common in a warm room and of 31° to 36°C. in a cold room. The lower normal temperatures grade into those of slight torpor at about 29°–32°C. The highest animal temperature recorded, 42.3°C., in a heated chamber was probably very close to the highest the animal can endure. The fluctuations in body temperature appear to be produced largely by changes in the surrounding temperature, but partly by the animal's activity and its rather poorly adjusted heat regulating mechanism. Vigorous exercise or confinement in a heated environment may cause a marked rise in body temperature (Johnson, 1928).

That this lack of temperature regulation and the accompanying power to hibernate is not a recent acquisition is indicated by the work of Martin (1901) on the spiny ant eater (*Aechidna*) and duckbill (*Ornithorhynchus*). These egg-laying animals are the lowest living representatives of the mammals. In *Aechidna* there was a fluctuation of 10°C. in the body temperature when the environment varied from 5° to 35°C. In *Ornithorhynchus* the temperature was low but more constant than in *Aechidna*. Martin found evidence for modification of both heat production and heat loss in *Ornithorhynchus*, and still greater heat control in marsupials.

Rectal temperature records (unpublished) taken almost daily on an adult male opossum, mostly in December, 1926, showed temperature variations in five readings ranging between 33.6° and 35.5° when taken in a room of between 25° and 29°C. The same animal removed to a refrigerator temperature of 4° to 6°C. showed a range of temperature varying from 33.5° to 34.7°C. A young opossum in a room temperature of 14° to 19°C. in February, 1925, showed a range of rectal temperature varying from 33.2° to 35.0°C. Two other opossums under the same conditions gave single temperature readings of 36.0°C. No hibernation was observed in four opossums in a cool cave nor in one kept at about 5°C. in a refrigerator.

Four pocket gophers (*Geomys bursarius*) kept in a cold room of about 4°C. for five days showed only slight temperature fluctuation, in one case 33.8° to 35.2°C. and in another case 35.2° to 35.8°C. The four died in a few days and like others kept in the refrigerator at other times never hibernated. A dying animal showed a rise of body temperature from 19.5° to 23.0°C. with a rise in heart beat from 40 to 124, on

removal to a warm room. As the animal died this was probably only a temporary rise in metabolism produced by the warming of the animal, and the lowered temperature cannot be considered hibernation.

Since prairie dogs (*Cynomys ludovicianus*) have been reported to hibernate only for short periods in nature it was felt that a study of their temperatures would be interesting. Forty-six daily records on seven animals in the cold room ranged chiefly between 32° and 36°C., whereas 57 daily records on five animals in the warm room showed a relatively stable temperature at 36°–37°C. (Table 1).

Three prairie dogs in a refrigerator had temperatures of 27°, 28° and 28°C. and were therefore on the verge of torpidity. Among several prairie dogs kept in a refrigerator temperature of about 5°–12°C. for several weeks at a time only three cases of normal hibernation were observed. These animals were not

TABLE 1
Temperatures of Normal Prairie Dogs

	ANIMAL TEMPERATURES						
	31*	32	33	34	35	36	37
Number of records at refrigerator temperature 3°–10°C.....	1	5	8	9	7	14	2
Number of records in warm room, range about 22°–29°C.....	0	0	0	2	7	31	17

* Each degree given includes the decimals of that degree, thus 31 = 31.0° – 31.9°C.

completely torpid, but could move very stiffly and trembled like ground squirrels in the later stages of a disturbed awaking from hibernation. The rectal temperature of one was 21.5°C. at a room temperature of 9.5°C. The second had a rectal temperature of 19.4° in a room of 9.5°C. A third was found, partly torpid, at a room temperature of 4.4°C. In breathing it made a wheezing noise, but this stopped as it gradually recovered its normal temperature. A fourth animal was considered as in abnormal hibernation. It was partly torpid at 22.0°C. cheek pouch and rectal temperatures. This animal seemed to have much difficulty in breathing, and in the quarter hour it was observed its temperature fluctuated a little with exertions but showed no real rise. The next day, however, it had a rectal temperature of 30.0°C. and was more active, although somewhat sluggish. Again 13 days later this animal was slightly torpid at rectal and pouch temperatures of 29.5° and 29.3°C. respec-

tively. At this time it had difficulty getting air and its heart beat was somewhat irregular, showing pauses between a series of regular beats.

Incidentally, from these temperature studies it may be concluded that the opossum may possibly hibernate to a slight extent, that the pocket gopher does not hibernate, and that the prairie dog hibernates only for short periods in the coldest weather. In this connection also, it is of interest to note that young mice and rats do not regulate their own temperatures well until they are ten days old (Pembrey, 1895), and even a group of adults may have a range of 1.0° to 2.0°C. (Sumner, 1913). According to Biersens de Haan (1922) a rise of 5.0°C. in external temperature produced an average rise of 0.70°C. in the body temperature of 3½ week old rats.

TEMPERATURE IN HIBERNATION

Body temperatures lower than or equal to those of the surroundings have been reported in torpid bats by Hall (1832), in marmots by Valentin, according to Barkow (1846), and by Monti and Monti (1900). In torpid ground squirrels Horvath (1872a) reported a body temperature of 2°C. in a room of 2°C., (1878) of 11.8°C. in a room of 13°C., of 11.5°C. in a room of 12°C., and of 4.6°C. in a room of 5.8°C. Barkow (1846) made similar findings but like Valentin considers that body temperatures are usually a little higher than those of the surroundings. Saissy (1815) and others found the temperatures of torpid marmots, hedgehogs, dormice and bats to be higher than those of the room, the difference being 1° to 2°C. (Quincke, 1881), i.e., 0.5° to 0.8°C. in bats in a cave of 6.4° to 7.7°C. (Delsaux, 1887); 0.25° to 2.0°C. in bats (Pembrey and White, 1896); a few tenths of a degree in the marmot (Dubois, 1896); and 1.1° in ground squirrels in a box of 2.2°C. (Shaw, 1925b).

That serious errors could be made in the study of animal temperatures in relation to room temperatures became evident to the writer in the progress of his work. The causes of these errors were eliminated by meeting the following conditions: constant room temperature, room temperature taken at the level of and near the animal, animal not in contact with a floor that was colder or warmer than rest of room, complete corrections applied to thermometers, animal and room temperatures taken immediately upon entering the room, animals disturbed as little as possible, light not used intermittently, and quietness in the hibernating room.

In a cold room (Johnson, 1928) when the temperature had become fairly constant after a gradual fall, three temperature curves of *C. r. pallidus* ground squirrels remained about 0.5° to 1.0°C. higher than the room temperature curves in three animals. Thermo-

couples placed in the bottoms of thick corkboard nests indicated body temperatures of a little less than 1.0°C . (0.5° to 1.2°C . in 92 per cent of 144 records) above that of the surroundings in ground squirrels long in deep hibernation. Of 25 records obtained by removing torpid ground squirrels from a refrigerator and immediately taking their pouch temperatures thermoelectrically, 40 per cent were less than 1.0° higher, 68 per cent were less than 2.0° higher and all the records were less than 4.0° higher than the refrigerator temperature, which ranged from 4.9° to 8.4°C . Torpid ground squirrels appear, then, to be usually about 1.0° to 3.0°C . warmer than their surroundings, but they are often less than 1.0°C . above, and may be rarely only 0.3°C . above the surrounding temperature. That Horvath and Monti and Monti and some other workers failed to observe proper precautions seems evident. The metabolism of the animal is sufficient to keep its temperature slightly above a constant surrounding temperature.

The lowest temperature in a torpid woodchuck observed by Dubois was 4.6°C . He states that the temperature of bats may fall to 5.0°C . or even to 1.2°C . in hibernation. Horvath (1872a) gives the lower temperatures of hibernating ziesel as 2.0° and later (1881) as varying between 1.8° and -0.2°C . The animal with a temperature of -0.2°C . woke up as a result of an external temperature of -0.5°C . As has already been pointed out, some of Horvath's temperatures were possibly not reliable; hence these may not be either. The lowest temperature given by Horvath was recorded during a falling outside temperature and may have been taken near the surface of the body; the emergent stem may have slightly lowered the reading, or the thermometer may not have been accurate. Dubois (1896) states that Brehm found temperatures of bats as low as 1.2°C . Adler (1926) states that if bats are cooled carefully and are not disturbed by touching or noise, their temperature may be lowered to 0.5°C ., but that this temperature usually starts the awakening process.

That animals in hibernation may approach the freezing point of water was evidenced in my work (Johnson, 1928) in which a *C. t. tridecemlineatus* was observed with a food pouch temperature of 2.0°C . in a room of 1.0°C . This animal woke in a normal manner. That death results somewhere between 2.0° and 0.0°C . was indicated by the fact that one *C. t. pallidus*, which was almost dead, had a temperature of 0.2°C . (Johnson, 1928). It did not respire for an hour and had a very slow and abnormal awakening. An animal with a temperature of 0.0°C . breathed very slightly after 22 minutes but did not wake up. In several instances where the refrigerator temperature

fell to 0.0° or slightly below, the torpid ground squirrels died. Semper (1881) reviews some reported cases of survival of frogs and other animals when frozen, but concludes that there is insufficient evidence especially that the tissues, blood, etc., were actually frozen even though the external temperature may have been much below freezing.

The death of torpid animals at freezing temperatures in this and other laboratories (e.g., Hunter, 1837) casts doubts upon the conclusions of Barkow (1846), Valentin (1857), Horvath (1881), Dubois (1896) and others that such temperatures always produce waking of a torpid mammal. Experiments have been reported (Johnson, 1929b) which showed that a lowering of the external temperature from about 3° or 4°C ., to 1°C ., woke some of the ground squirrels (*C. t. pallidus*) but not all, and those which woke usually went back into normal hibernation with the air temperature at 1.0°C . These animals were observed frequently, so it was not possible that any woke and went back into hibernation without being observed. Wade (1930) found that a rapid drop in room temperature to -1.0° or -2.2°C . woke most but not all his ground squirrels, some dying without awakening.

RESPIRATION IN NORMAL ANIMALS

Saissy (1815) reported respiration rates of 30, 16, 45 and 7 respectively per minute for the marmot, hedgehog, dormouse and bat at 16°R . (20°C .) in August. Barkow (1846) counted 20 to 40 respirations in sleeping hedgehogs. A surprising range has been found in ground squirrels (Johnson, 1928). Among 48 *C. t. tridecemlineatus*, there was a range of 45 to 340 inspirations a minute, with an average of 187. In 37 awake and quiet *C. t. pallidus*, respiration varied from 20 to 360, with an average of 126 a minute, while a group of 12 others, after moving or feeding averaged 213 a minute, individuals varying from 140 to 320. A rate of 100 to 200 has been considered as most common in either variety of ground squirrel. Hoy's (1875) rate of 50 a minute for ground squirrels was probably from an inactive or semi-sleeping animal, since my observations on sleeping animals gave a range of 7 to 68, with an average of about 25 a minute in the two varieties of squirrels. In addition to degree of excitation, the variation in respiration rate in ground squirrels may be largely accounted for by the existence of a slow type of inspiration, involving a great but slow expansion of the whole thorax when the animal is quiet, and of a rapid shallow expansion of the abdomen and posterior thorax seen when the animal is excited or very active.

RESPIRATION IN HIBERNATION

Mangili (1807) found respiration to be very irregular in hibernation. He reported a 15 minute pause in the respiration of the hedgehog followed by 30 to 35 slow respirations. In dormice at 1°C. he recorded 147 inspirations in 42 minutes but with pauses of 3 to 8 minutes. In other series of records the pauses ranged between 2 and 13 minutes and between 3 and 5.5 minutes.

Some correlation between temperature and frequency of respiration in hibernation was seen by Saissy (1815). In hibernation that he considered was not very deep the respiration counts per minute were 7-8 for the marmot, 4-5 for the hedgehog, 9-10 for the dormouse, and either 0 or 4-5 for the bat. In deep hibernation he saw no breathing in the bat and considered this to be the general rule with other animals in deep hibernation. Hall (1832) and Delsaux (1887) observed no respiration in very torpid bats but the latter found that they gave off 394-615 mgm. CO₂ per kgm. per hour. It must be admitted there is a greater possibility of absorption of oxygen through the thin skin of the wings of a bat than through the skin of other mammals. Ziesels at 2.5°C. body temperature and undisturbed torpid hedgehogs had no visible respiration according to Barkow (1846). Dubois (1896) observed 1-4 very feeble respiratory movements a minute in profoundly torpid marmots.

While pauses in respiration have been noted in torpid ground squirrels, absence of respiration for several minutes is probably abnormal (Johnson, 1928), for two animals that showed no respiration until 14 and 25 minutes respectively after removal to a warm room died after a slight breathing for a few minutes. Two others which respired only after 19 and 22 minutes recovered abnormally. A fifth, which showed no respiration for an hour, recovered very slowly with the aid of artificial respiration. From careful observations, it was concluded that in deeply torpid ground squirrels in a room below 10°C., inspirations may average from one-half to four a minute normally, but that they may fall somewhat lower in thin animals long in hibernation.

To determine the ability of poikilothermal mammals to endure the lack of air while in the active state Carlisle (1805) kept a hedgehog under water of 8.8°C. for 30 minutes, but apparently the animal had its nose to the surface a number of times. It recovered in two hours, whereas another kept under water of 34.4°C. died in 10 minutes, due possibly to the higher rate of metabolism when warmer. Barkow (1846) states that the normal hedgehog may sometimes endure total immersion for eight minutes, but others died in 3, 4 and 5 minutes. Hall (1832) also

states that normal bats and hedgehogs drown in about 3 minutes, but two torpid bats were under water 11 and 16 minutes and a hedgehog 22.5 minutes without injury. Poisonous gases did not injure torpid bats and marmots according to Spallanzani (1803) and a hedgehog could endure nitrogen gas for 15 minutes, whereas the mouse, rat and sparrow died respectively in 2.5, 2.5 and 0.5 minutes (Saissy, 1811). Saissy also found that a hibernating animal could use up all the oxygen in a closed chamber before suffocating, whereas the rabbit absorbs only 75 per cent, the rat only 62.5 per cent, the sparrow only 42.5 per cent before dying. Delsaux (1887) showed that normal bats placed in a chamber in which the air was rarified by means of a vacuum pump to 50 mm. of mercury appeared asphyxiated, but could remain in this condition for half an hour and still recover when removed.

Delsaux (1887) reported Regnault and Reiset as finding that a marmot used only one-thirtieth as much oxygen when torpid as when awake. According to Dubois (1896) Valentin reported that a torpid animal used one-forty-first as much oxygen and eliminated one-seventy-fifth as much carbon dioxide as a normal animal. Pembrey (1903) found that the relation of the carbon dioxide excreted in hibernation (body temperature 12° to 16°C.) and in activity was about 1:100 in the dormouse and 1:10 or 1:20 in the hedgehog. Gorer (1930) points out that the highest metabolic rates of hibernating mammals were reported by Pembrey for the dormouse, about 300 cc. oxygen per kgm. per hour being absorbed when torpid at 10°C. as compared to about 8,000 cc., about 27 times as much, when awake. For the marmot the amounts were about 35 and 550 cc., about 1:16 at 10°C. and awake, respectively. Stockard (1930) gives the carbon dioxide output of a white tailed prairie dog (*Cynomys leucurus*), in hibernation November 15 at a body temperature of about 21°C., as less than one-eighth that of the same animal two and three days later when sleeping or awake but quiet at a body temperature of about 32°C. (The date and temperatures have been kindly provided by Mr. Stockard in a letter to the author.)

In studying the effect of hibernation upon the respiratory quotient ($\frac{\text{CO}_2}{\text{O}_2}$) Dubois (1896) found that more O₂ was absorbed than was represented in the CO₂ given off and the respiratory quotient approached 0.5, and he states that Regnault and Reiset found it to be as low as 0.4, whereas in the animal awake or in the process of waking it approached unity and even exceeded unity at the very beginning of waking. Pembrey (1903) found a respiratory quotient as low as 0.23 and 0.50 in torpid dormice and hedgehogs, re-

spectively. According to Gorer (1930) several workers object to low quotients, but he concludes that the real quotient must be below 0.7 and believes that it ranges from 0.3 to 0.5. A low respiratory quotient according to Pembrey (1903) and Bayliss (1918, p. 278) indicates that there is a conversion of fat, which contains a small amount of oxygen, into carbohydrate, which contains more oxygen. Gorer (1930) considers the significance of the respiratory quotient at some length but concludes that direct evidence on the metabolism is needed and would help to determine the quotient.

HEART BEAT IN THE NORMAL AND HIBERNATING STATES

In active bats a pulse rate of 200 a minute was reported by Prunelle (Barkow, 1846). Rates of 90 a minute in a room of 19°C. and of 30 a minute just before hibernating in a room of 6°C. were found by

From the slight bleeding when a vessel was cut and from the lack of enlargement when vessels were tied in the neck and legs, Saissy (1815) concluded that there was no peripheral circulation in deep hibernation, but merely a slight ebb and flow in the vessels near the heart. He was supported in this by Brown (1847), who also agreed with Mangili (1807) that little blood reached the brain in torpor. Dubois (1896) maintained that a very slow circulation is present in hibernation, a view shared by the present writer.

Instances of heart-block, or the independent beating of auricles and ventricles, have been cited by Buchanan (1911) as occurring in the partly torpid dormouse. A complete missing of beats of the heart has been shown in an electro-cardiogram from a ground squirrel which had begun to awake from hibernation (Johnson, 1929b).

The rate of heart beat in normal ground squirrels varies greatly (Johnson, 1928). In both varieties

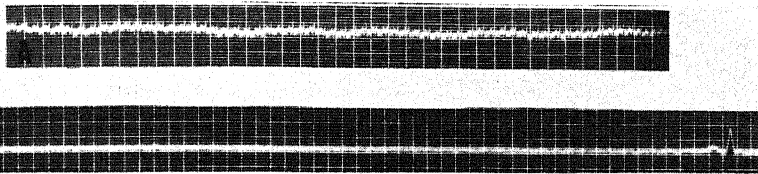


FIG. 1. A. ELECTROCARDIOGRAM OF *CITELLUS TRIDECIMLINEATUS PALLIDUS*, No. 947, STRUGGLING AND BITING, SHOWING 506 BEATS A MINUTE. LEAD I, TWO ARMS. B. ELECTROCARDIOGRAM OF *C. T. PALLIDUS*, No. 938, IN DEEP HIBERNATION, SHOWING 1 BEAT IN 10.32 SECONDS OR 5.53 BEATS A MINUTE. LEAD I, TWO ARMS. TIME 3:03.

Saissy (1815), and of 28 a minute in hibernation by Hall (1832).

In active dormice Reeve (1809) states that the rate is too rapid to count but falls to 88 a minute in beginning torpor, or to 105 at 19°C. and 88 a minute at 6°C. (Saissy, 1815). In deep torpor it falls to 16-20 (Reeve, 1809), 20-25 (Saissy, 1815), or 10-12 a minute (Spallanzani, by Barkow, 1846).

In hamsters pulsation rates of 150-200 (Sulzer, by Barkow, 1846) in activity or of 100-150 when irritated (Reeve, 1809), fall to about 60 before hibernation and as low as 12-15 in deep torpor (Reeve, 1809; Sulzer, by Barkow, 1846; Dubois, 1896).

Hedgehogs may have a pulse rate of 75 a minute in a room of 19°C., falling to 25 at 6°C. At these temperatures a marmot had 90 and 70 beats a minute respectively (Saissy, 1815). In torpor the marmot was found to have a pulse rate of 27-28 a minute (Mangili, 1807), but this rate may have been raised by the decapitation and opening of the thorax, for Saissy (1815) gives a rate of 10-12, and Dubois (1896) has made some cardiograms with a rate as low as 3-4 a minute in torpid marmots.

the range was found to be about 100 to 200 in animals just awakened from normal sleep, but rose to 200 to 350 in animals held, some quiet and some struggling. In excited struggling animals the rate often rose above 350, rates of approximately 400 being sometimes recorded by counting the beats in an abbreviated manner with a stethoscope. That the rate may go still higher is shown in Figure 1a, an electro-cardiogram of a *C. t. pallidus* ground squirrel biting and struggling violently while it was held showing 8.43 beats in one second or 506 beats a minute. This is 100 times as fast as the lowest rate (5 a minute) recorded in two very torpid animals (a cardiogram of 5.53 beats a minute is shown in Figure 1b). It is 29 times faster than the average (17.4 beats) of the 22 lowest records of animals whose temperatures were below 10°C.

SURVIVAL OF THE HEART

Several workers have observed the persistence of reflexes in decapitated hibernating mammals (Merzbacher, 1904) and the continued beating of the heart three hours after decapitation in a torpid marmot

(Mangili, 1807). A ground squirrel, *C. t. tridecemlineatus*, was dug out of its underground nest in the winter by the author and its heart beat observed within 8 minutes by cutting open the thorax ventrally. The heart beat was 13.5 a minute at first, the body temperature, 2.0°C., respiration rate, 2 a minute, and air temperature, 4.0°C. After 18 minutes the heart beat rate was 14 and the animal was taken into an air temperature of 0.0°C. After 47 minutes the heart beat had fallen to 6.5, with a body temperature of 5.5°C. and attempted respirations of 2.4 a minute. From 1:52 to 6:00 (taking the beginning of the experiment as 0:00 hour) the heart beat was irregular at about 2 to 4 a minute and attempted respiration stopped before 3:38. When removed to a temperature of 18°C. at 6:28 its heart beat rose to 9.2, 18 and 28 respectively at 6:38, 6:56 and 7:05. It was necessary to leave the laboratory, so the animal was then skinned. By 7:21 its heart beat rose to 61 a minute. The body was placed in 10 per cent formalin. The heart stopped beating in 30 minutes, which was seven and one-half hours after it was exposed. Another torpid ground squirrel, a *C. t. pallidus*, had a heart beat of 17 a minute when cut open, but this decreased to 6 in one hour and to 3 in two hours and ten minutes. At first the attempts at respiration were deep and frequent; the last slow and feeble attempts were noted one hour and 24 minutes after opening the thorax. The heart ceased beating sometime between two hours and ten minutes and four hours and 31 minutes after exposure. A second torpid *C. t. pallidus*, with a heart beat of 15 a minute when the thorax was cut open, showed great efforts to expand the thorax and the heart beat increased to 17 in 7 minutes, but by 23 minutes the expansion of the thorax was slight and the heart beat 10 a minute. The heart beat fell to 7 in one hour, 6 in 2 hours, 3 in 5.5 hours and stopped before 8 hours. In the last two experiments the room temperature averaged about 4°C.

The beating of the heart of the torpid animal several minutes after isolation and placing in warm Ringer's or salt solution has also been confirmed by the author. Merzbacher (1904) states that the heart of a hibernating mammal will beat for hours if excised and kept cold and moist.

Death in hibernation appears to be produced by cessation of respiration rather than of heart beat, for the heart was still beating in five ground squirrels in which no respiration was seen for respectively 14, 19, 22, 25 and 60 minutes after the animals had been removed from the cold to a warm room. The first and fourth of these died after respiring slightly for a few minutes. The others recovered very slowly, were very weak and the last one would probably have died

if artificial respiration had not been resorted to (Johnson, 1928).

RESISTANCE OF TORPID MAMMALS TO TOXIC SUBSTANCES

Injected poisons produced little or no effect on torpid animals (Merzbacher, 1904). Hibernating bats were found resistant to pilocarpin, apomorphine and strychnine by Koennick, according to Adler (1926), who compares this resistance when the animal is not awakened to that of cold blooded animals. Blanchard (1903) found that torpid marmots were sensitive to inoculations of trypanosomes and to toxins of tetanus and diphtheria as well as to venom of the cobra. Hibernation merely slowed up the action of the toxins, for they were nearly as deadly to the torpid as to the normal animals.

IRRITABILITY IN HIBERNATION

While the nervous system of a torpid mammal functions to maintain a low rate of heart beat and of respiration, it becomes progressively less sensitive to stimuli as its temperature falls. Before this falls to about 30°C. thirteen-lined ground squirrels can move and respond to stimuli in practically the normal way. When it has fallen to about 20-30°C. they may move forward in a dazed manner or merely raise up stiffly and try sluggishly to bite when touched. At about 10°-15°C. the animals are more inert and are likely only to raise the head slightly or give other weak responses. If the body temperature falls to about 2°-5°C. there is usually no response even to strong mechanical stimuli such as inserting a thermometer bulb into its food pouch or pricking the animal with a needle. At low body temperatures Franklin, Richardson and *Callospermophilus* ground squirrels have been observed by the author to be as unresponsive as the thirteen-lined species. Hatt (1927) made similar observations on the *Callospermophilus* and Shaw (1925c) on the Columbian ground squirrels. Touching a torpid hedgehog caused it to breathe eight to twenty times, the respirations gradually becoming shorter and slower and the animal did not wake unless the stimulation was continued or the animal taken to a warm room.

While the immediate responses may not be made to such severe stimuli as falling from a table and breaking a collar bone or by having the nose cut open to expose nerves and blood vessels as in a young marmot (Valentin, 1857), stimuli of this strength would invariably wake a ground squirrel in due course of time. However, it is often possible to gently lift a deeply torpid ground squirrel out of the nest and

carefully insert a thermocouple into its food pouch without causing it to wake (Johnson, 1928).

Horvath (1881) states that conditions in hibernation may vary somewhat in different groups of mammals. In *Myoxus dries* he found that the eyes were not closed as in ground squirrels, and the hamster might give forth loud cries, or more probably, draw in deep sonorous inspirations when disturbed as stated by Cleghorn (1910). The degree of immobility in bats may vary with the temperature, time of year and the species according to Dubois (1896) and others. Black tailed prairie dogs and a pocket mouse in partial hibernation with a body temperature somewhat above 20°C. were observed by the author to straighten out and make feeble attempts to crawl when held in the hand. If the temperature in these two forms can fall to 2°-5°C. it is probable they would be as inert as ground squirrels.

Electrical stimuli produced no effect on woodchucks and hedgehogs but caused slight movement on the part of dormice and bats (Saissy, 1815). Marmots were not roused by an electric spark and they were excited only for a short time by a shock from a Leyden jar according to Reeve (1809) and earlier workers quoted by him. If the electrodes were placed directly on the exposed muscles or nerves that go to them, Horvath (1872b) found that the cold muscles responded even to weak induction stimuli. Electrical stimulation of the exposed cerebral hemispheres of torpid bats produced no effect on one bat, but on another strong stimulation (coil at 6 cm.) caused inhibition of respiration for ten minutes (Merzbacher, 1903a). By stimulation of torpid ground squirrels by means of shocks from an induction coil (Harvard inductorium) the author has produced movements, such as raising of the body or even the turning of the head, which had not been produced by mechanical stimuli at the same temperature.

While considerable variation has been seen both in the tendency to hibernate and in the irritability in hibernation among large numbers of the same species of ground squirrels observed, it nevertheless appears that there is a marked general relation between body temperature and activity. This is especially evident in the regaining of powers of motion as a torpid animal wakes, observed by many authors. Britton (1922) has shown that even in a cat cooled to the point of lethargy the muscular activities return in a certain order and at somewhat definite

body temperatures as the animal recovers, although such non-hibernating animals lose their power to respond to stimuli at a higher body temperature when that is lowered artificially. The production of immobility, whenever an animal's body temperature falls, suggests that the bear and possibly the raccoon do not actually become torpid, for Dubois (1896) and Bailey (1926) state that they are easily aroused, which could hardly be the case if the body temperature is very low.

EFFECT OF HIBERNATION ON WEIGHT

All workers have recognized that loss of weight in hibernation is small as compared to that in starvation and have pointed to this conserving action of lethargy as its chief function. While it is also generally recognized that there is a considerable loss in body weight in an extended period of hibernation, there is no marked agreement as to the exact loss. Bailey (1926) believed there was "only slight loss of fatty tissues." He considered the lack of food after waking and during the breeding season as drawing heavily upon the stored fat. In pocket mice and some chipmunks he observed no accumulation of fat but called attention to their stores of seeds and grains which he believed they consume at intervals of awakening. Earlier workers have generally considered that animals are fat in the fall and wake up lean in the spring, as reported for the dormouse by Murray (1826) and several others.

Marmots lost one-fourth to one-sixth of their body weight in about 130-150 days of hibernation and in two animals even in 56 and 59 days respectively, and two hedgehogs¹ lost one-fourth of their weight in 26 and 50 days respectively (Valentin, 1857). Wade (1930) has estimated that one-half of the weight may be lost by ground squirrels which den up in late summer, and some of his records (p. 173) show losses of 59 and 61 per cent in 207 and 228 days in which the animals' burrows were closed.

The weight losses of five *C. t. tridecemlineatus* which hibernated outdoors have been studied by the author. Estimating that they changed little in weight in the four to six weeks before hibernating (they were fed well, but they also exercised considerably in digging burrows and building nests) the losses from the time of closing their burrows till they were dug out in the torpid state were: 19 per cent in 65 days; 21 per cent in 83 days; 18 per cent in 106 days; 32 and 39 per cent in 100 days. A *C. t. pallidus* lost 38 per cent in 79 days. As none of these animals hibernated as long as animals would in nature, this average loss of 28 per cent is probably lower than occurs in nature. The average daily loss was 0.32 per cent. A comparison of average weight (93 grams) of 120 *C. t. pallidus* received early in the spring with that (157 grams) of 45 adult laboratory animals which were not excessively fat in the fall would indicate an average loss of about 41 per cent from fall to spring (Johnson, 1928).

Ground squirrels which refused to hibernate when placed in a refrigerator showed marked losses if fed sparingly, but lost less or even gained slightly when fed well (Johnson, 1928). Where two or more weight records were obtained within a period of hibernation in which waking was believed not to occur, the average daily loss in eight records of 14 to 17 days was 0.57 per cent. If the loss were computed on this basis, calculating it on the reduced weight each 15 days, the animal would lose 45 per cent of its original weight in 100 days, and 59 per cent of its original weight in 150 days. Five other animals whose periods of hibernation averaged 28 days lost 0.43 per cent daily. If the successive reductions in weight are used and the losses computed in periods of 25 days each, an animal in 100 days of hibernation would lose 36 per cent, and in 150 days, 49 per cent of its original weight.

Seven *C. t. pallidus* ground squirrels were placed in a refrigerator August 5 and removed January 8, 1956 days later. They were in hibernation an average of 83 per cent of this time. Five of these animals which were in good condition, weighing 147-185 gm., when placed in the refrigerator, were taken out somewhat thin, having lost 37 to 49 per cent (average 45 per cent) in weight. Two which had been very fat lost respectively 40 and 39 per cent of their original weights of 226 and 250 gm., but were still somewhat fat. Considering that the loss in hibernation in a closed underground burrow may be less than in a refrigerator, the data presented would appear to indicate that ground squirrels commonly lose 30 to 45 per cent of their weight in five months of hibernation in nature.

The loss in weight during hibernation is accounted

for chiefly by the using up of the thick layers of fat under the skin, in the mesenteries, and in the mesovaria or mesorchia. In the fall the latter may be 4 mm. in thickness, their appearance suggesting thick pieces of bed quilts, but in the spring the fat may be reduced to streaks along the blood vessels which course through the epithelium to the reproductive organs (Johnson, 1928). Williams (1909) has called attention to the localization of "a heavy fat blanket" on the more exposed hind quarters and back in the hibernating raccoon. He found more than one-fourth of the body weight to be fat.

Slight temporary increases in weight have been reported by Horvath (1878), Dubois, (1896) and others, but this condition was attributed by Valentin (1857) to absorption of moisture by the fur rather than to fixation of oxygen with retention of carbon dioxide as mentioned by Pembrey and White (1896) and others. Valentin (1857) also discovered gains in weight in animals that had awakened between weighings.

THE PROCESS OF WAKING FROM HIBERNATION

Types of awaking

Two types of awakening from hibernation have been described (Johnson, 1929a):

(a) A relatively rapid awakening accompanied by trembling and shaking of the head and shoulders, following a disturbing of the animal by removing it from the nest and laying it on the side or back, and either taking it to a warm room or leaving it in the cold room; (b) A more gradual awakening, usually without trembling or shaking, after removal without disturbance to a warm room, or following some handling at first after which it was placed back in the rolled up position in the nest and left in the cold room.

In the first type of awakening the breathing increased in rate, the body showed some movement of forefeet or head or of both, then more marked movements such as trembling, shivering, shaking the head sideways or jerking it up and down. These movements were accompanied by a gradual straightening of the body from the rolled up position and were

usually followed by deep, rapid and convulsive respirations, and later by the raising of the head, the getting up on the forefeet, and still later by standing on all fours. Before or at this time they became very irritable and could fight in a drunken but determined manner. Soon the eyes would open and if disturbed they would move forward, awkwardly for a few minutes. If the animal was transferred to a warm room in addition to being stimulated by being laid on its side and having its temperature taken, the steps mentioned were crowded together and the stages given might occur two at a time. This type of waking has been described in various forms by Pembrey and Pitts (1899), Hahn (1914), Dubois (1896), Shaw (1925b), Hatt (1927) and others. Merzbacher (1903) has described four stages in the return of activity in a bat waking from hibernation. These were: (1) rigidity, with only reflexes of the spinal cord; (2) hanging on, with reflexes of the medulla oblongata; (3) beginning of cerebral activity with loss of sub-cortical reflexes and accompanied by the opening of the eyes; (4) fully awake, with cortical control of sub-cortical reflexes.

In the second or relatively undisturbed type of awakening there was much abbreviation and elimination of the steps given for the first type. Increased respiration or a raising or humping of the rolled up body was often followed by a working out of the head from underneath, then by raising the head and opening the eyes accompanied by standing on the forefeet. While this type of awakening is probably typical of that in nature, the disturbed type has been the one usually described.

The opening of the eyes occurred usually in the disturbed awakening between 20° and 34°C. in 12 *C. t. pallidus* and 15 *C. t. tridecemlineatus*, and in the undisturbed type it occurred between 21° and 37°C. in 45 *C. t. pallidus*. The difference in temperature at

waking therefore was not great. However, the 27 disturbed animals woke in 63 minutes on the average, whereas the undisturbed animals woke in an average of 114 minutes.

Effect of stimulation during waking

While strong stimulation at first is almost certain to produce complete awakening even in the cold, showing that irritability is not completely lost in deep torpor, even if no quick response is seen, it is interesting to note that continued stimulation during the waking by dropping small weights on the animal or by applying electrical shocks with an inductorium did not hasten the process very much and sometimes caused inhibition of the heart beat and respiration for a short time.

Mid-brain necessary for waking

Dubois (1896) found that destruction of the cerebrum and corpora quadrigemina did not prevent waking from hibernation, but a destruction of the mid-brain prevented waking. With only the medulla oblongata left the torpid marmot would live 8 to 9 hours or more but could not awake automatically and died while torpid.

The rise in respiration, heart beat and temperature

When waking from hibernation is started by some external stimulus the heart beat seems usually to take a slight lead over respiration in producing a warming of the animal (Johnson, 1929b). Figure 2 illustrates the increases in respiration, heart beat and temperature in disturbed waking in a cold room (Ia, IIa, IIIa), in a moderately warm room (Ib, IIb, IIIb), and in an unusually warm room (Ic, IIc, IIIc). It is seen that the rise in metabolism is slow at first in the cold room (a) but speeds up considerably at about 60 minutes. In the moderately

warm room (b) the rate is rather steady throughout, the respiration and heart beat showing a very great increase after 35 or 40 minutes. In the warmest room (c) the temperature rise is very pronounced as soon as the animal is removed from the cold to the warm room, indicated by the

animal is fully awake, as was stated by Dubois (1896). In about 35 minutes after the animals, I, J, K and L, were taken to the very warm room (Ic) the respiration rate rose from about 8 a minute to about 150, the heart beat rose from 28 to 375 a minute, and the food pouch temperature

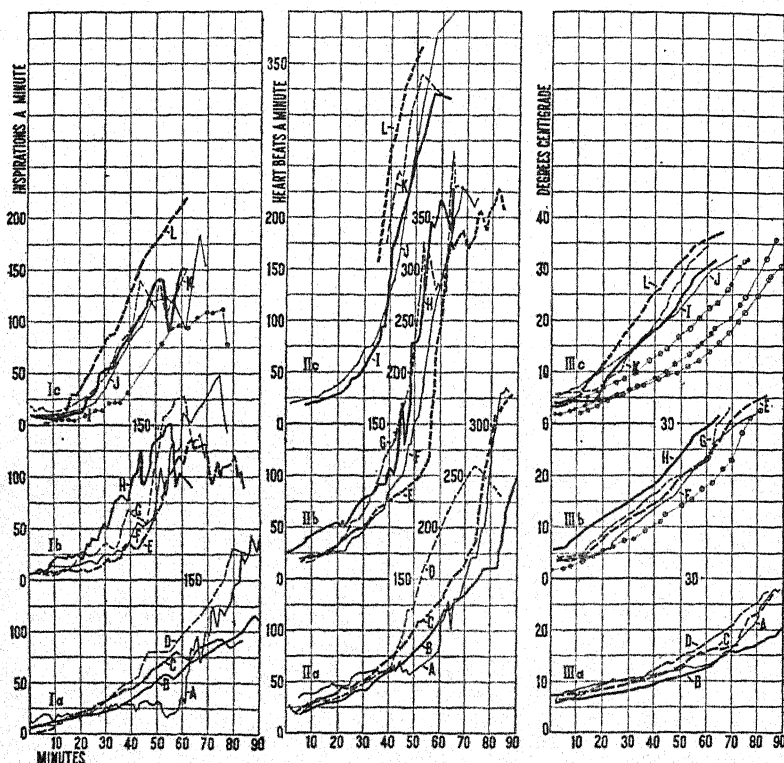


FIG. 2. GRAPHS OF INCREASE IN RESPIRATION (I), IN HEART BEAT (II) AND IN TEMPERATURE (III), IN A COLD ROOM OF ABOUT 2° TO 10°C . (a), IN A ROOM OF ABOUT 15° TO 22°C . (b), IN A WARM ROOM OF ABOUT 25° TO 35°C . (c)

The curves belonging to one animal are designated by the same capital letter, thus I a A, II a A and III a A represent the respiration, heart beat and temperature increases respectively in one waking process in the cold room of the animal A. The fine lines connecting the rings in I c, III b and III c are graphs of animals waking relatively undisturbed (thermocouple gently placed in the food pouch and the animal replaced rolled up in the nest). In the other graphs the animals were disturbed by being straightened out and by taking of heart beat in addition to temperature.

abrupt rise in the temperature curves at 5 to 10 minutes in the graphs. There is the same rate of increase in heart beat at about 25 or 30 minutes in the warmest room that was observed in the medium warm room ten minutes later. Heart beat may be more rapid at this time than when the

from about 7° to about 27° , or 20° in 35 minutes, or 0.57°C . a minute. In the undisturbed awakening of two animals (Fig. 2, fine lines connecting the rings in IIIc) the rate of rise of temperature was about 19° or 20°C . in 40 minutes, about 0.5°C . a minute, after the rise was well begun.

Dubois (1896) gives some graphs of respiratory movements showing a rising rate as waking progresses. Other graphs of the waking dormouse showing pauses followed by a series of inhalations (Biot's type) and pauses followed by increasing depth of inspirations then decreasing again to another pause (Cheyne-Stokes respiration) were shown by Pembrey and Pitts (1899).

Several references to rate of temperature rise in waking were found in the literature. From these records the average rise has been calculated and is substituted here. For a portion of its waking period the bat may warm up about 1.1° – 1.6° C. a minute (Pembrey and White, 1896; Pembrey, 1898). Ground squirrels (ziesels) may warm up 0.26° and 0.38° C. (Horvath, 1872a), 0.40° – 0.45° C. (Horvath, 1878), or 0.30° C. (Mares, 1892) a minute. Dormice may warm up 0.37° (Pembrey, 1898) or 0.95° C. (Pembrey and White, 1896) a minute. Hedgehogs, which are larger, warm more slowly, 0.17° a minute (Pembrey, 1903), while the still larger marmots require three or four hours to warm from about 5° to 30° C., a rate of about 0.10° to 0.14° C. a minute. Most of these records were based on rectal temperatures and it has been shown that this lags far behind the esophageal, mouth or pouch temperatures (Quincke, 1881; Dubois, 1896; Mares, 1892; Shaw, 1925c; Johnson, 1929b; and others) and apparently catches up with the esophageal and pouch temperatures late in the waking process (Dubois, 1896; Johnson, 1929a, p. 179) especially in the cold room. This late rapid rise in rectal temperature appears to be produced largely by a sudden increase of circulation to that region after the anterior region has gradually warmed up from the beginning of waking, for Mares (1892) showed that jugular injection of indigo-carmin in a torpid ziesel quickly produced intense blue staining in the skin and mucous membrane anteriorly but not posteriorly. For the reasons given rectal temperatures are not reliable indicators of the rate of rise of metabolism but have been included here because they have some value in comparison between species.

The time required for waking from complete torpor depends somewhat on the size of the species. The following observations of waking time have been reported: (1) for the bat, 14 or more minutes (Pembrey and White, 1896; Pembrey, 1898), "a few minutes" (Adler, 1926), a half to one hour on the snow (Mangili, 1807), and three or four hours (Saissy, 1815; Quincke, 1881); (2) for the hedgehog, five to six hours (Saissy, 1815; Quincke, 1881); (3) for the marmot, three to four hours (Dubois, 1896), five to six hours (Quincke, 1881), and eight to nine hours (Saissy, 1815). These rates would probably be less variable if the observations had always begun at a

certain body temperature and ended with the return of voluntary activity, and also if esophageal or food pouch temperatures had been taken.

The energy consumed in a unit time in waking ziesels has been stated to be 70 per cent greater than in the normal state (Mares, 1892). Mares found that during waking 5.9 gm. of oxygen per kilogram per hour were absorbed as opposed to 3.8 gm. in the normal state, and 6.0 gm. carbon dioxide are exhaled in waking compared to 3.9 gm. in the normal state. Pembrey and White (1896) noted the sudden increase in temperature just at the point of waking in bats, and this was observed to be accompanied by a much greater rate of heart beat and respiration at about the time of opening the eyes in ground squirrels (Johnson, 1929b) than was found after the animal was fully awake but not excited. The contraction of the heart, the movement of the thoracic muscles and the trembling, which may be present, appeared to account for the rapid rise in temperature in the latter part of waking. Mares (1892) considered that burning of fat produced this, but Dubois (1896) considered that glycogen in the liver was converted into sugar and this was burned. Further evidence of a great increase of sugar in the blood early in awakening has been submitted by Dworkin and Finney (1927). In waking there appears to be a vicious cycle. As the heart beat increases because of stimulation it is accompanied by more rapid respiration, both processes producing heat. Increased heat and greater muscle contraction both demand more oxygen. The excessive increase in metabolism in waking suggests to the author that the heat regulating mechanism is rather sharply brought into play after waking has progressed somewhat, for once the waking process is well started, placing the animal back in the cold and leaving it undisturbed almost never prevent complete awakening.

GOING INTO HIBERNATION

While the literature contains references to going into hibernation no exact data have been presented as to the physiological changes that occur, probably because study at this time almost invariably awakens the partly torpid animals. Dubois (1896) states that a marmot may wake in 3–4 hours, but requires 4–5 times as long to go into hibernation. Hatt (1927) states that a *Callospermophilus* might go into hibernation in 6 hours. Hibernation is always entered from a condition of normal sleep. The author took a great many food pouch temperatures of *C. r. pallidus* ground squirrels at intervals of one or two to several hours after the animals were placed in a refrigerator. The gentle picking up of the animal and careful insertion of the thermocouple in some cases did not prevent the

entrance into hibernation and the pouch temperature dropped from 1° to 3° an hour (Johnson, 1929c). Further work showed that it might drop 5°C. or even more an hour.

By taking temperatures thermo-electrically (illustrated in Johnson, 1929a) without disturbing the animal at all at the time the record was taken, drops of 6° to 7°C. an hour were observed for short periods in partly torpid animals in a rapidly falling room temperature, but the pouch temperature remained 1° to 2°C. above that of the room (Johnson, 1929c) even remaining 1°C. or more above when the room temperature stopped falling. From these data it was concluded that a fall in animal temperatures of 4°C. or more an hour was not uncommon.

The drop of 1° to 5°C. an hour in the early part of becoming torpid and up to 6° or 7°C. in short periods in the later stages is very much slower than the rise of 20° in 35 minutes in rapid awakening in a very warm room.

CONDITIONS IN HUMANS RESEMBLING HIBERNATION

A considerable lowering of temperature in a hysterical person sleeping after being hypnotized was reported by Mares (1892). Fakirs in India have been often reported to be revived after months of burial underground (Busk, 1885; Mills, 1893, and others), but, while attested to by English officials, the possibility of deception by the fakirs has been raised (Hulk, 1885, and others). According to Claparède (1905), Cleghorn (1910) and other writers, in times of famine in some parts of Russia the peasants may conserve food by voluntarily sleeping for four or five months, doing only the necessary things and eating very sparingly. While metabolism is probably lowered in this way, it seems doubtful if there is much lowering of body temperature. Cushing and Goersch (1915) have described symptoms of slightly lowered temperature and excessive adiposity in humans with deficient pituitaries and have considered this state related to hibernation. Mills (1892) also reported cases of excessive sleeping in two feeble minded men and in a woman who was tuberculous and had many adhesions of organs. Lowered temperature and drowsiness might, it would seem, be the effects of the illness rather than a condition resembling hibernation. Cases of lowered temperature in dying pocket gophers could easily be mistaken for real hibernation.

A CONSIDERATION OF THE POSSIBLE CAUSES OF HIBERNATION

There are certain outstanding facts regarding causes of hibernation. One is

the existence of a large number of theories, summarized by Rasmussen (1916a). Another is the tendency of some writers to go to extremes in denying the causative influence of some possible factors. Thus cold has been declared not to be a cause of hibernation (Merzbacher, 1904, and others). A fact which must be kept in mind is that a poorly developed heat regulating mechanism is a prerequisite to the ability of a mammal to hibernate, and since this is essentially a pre-mammalian characteristic, we may consider hibernation as something retained rather than acquired by hibernating mammals.

Many authors have sought for a single cause for hibernation, but many conditions, both internal and external, may influence entrance into it. The possible external factors in hibernation will be considered first, and then the internal conditions which may influence it.

Temperature

Among the external conditions a low temperature has been considered a cause by many (Brown, 1847; Quincke, 1881; Adler, 1926), but many others have pointed out that only moderate cold is favorable for hibernation and animals may die below freezing temperatures (Mangili, 1807; Adler, 1926); or they may be awakened at first at about the freezing point of water (Dubois, 1896; Mangili, 1807; Pflüger, according to Merzbacher, 1904), or hibernation may even be prevented sometimes (Valentin, 1857). Sudden severe cold may irritate and finally kill the animal (Dubois, 1896; Johnson, unpublished). Others have shown that animals in captivity may fail to hibernate in winter, even if in a cold place (Mangili, 1807) but may hibernate in the summer or early fall in cool but not cold surroundings (Horvath, 1881; Wade, 1930; and others). Some dormice kept over winter by Forel (1887) failed to hibernate until May, but as they did not become fat until that time their failure to hibernate earlier may have been caused by a poor physical condition. Simpson (1911-12) considered that woodchucks wake in the spring without a higher surrounding temperature.

Perhaps no investigator who has had a large number of animals under observation at one time would deny that animals hibernate more in a room of about 5° - 10°C. than in one of 20° - 25°C. , or even of 15° - 20°C.

This has been the experience of the author, who recognizes, however, that cold is not the only cause, and that internal causes may aid hibernation in ground squirrels in cool weather (20° – 22° C.) in the late summer, or hinder hibernation in cold weather (0° – 10° C.) almost any time of year but especially in the spring. In outdoor pens in Chicago ground squirrels kept their burrows open until periods of cold weather and snow in December, 1915. Hahn (1914) observed this in nature.

The idea that heat may be a cause of hibernation (Brown, 1847; Merzbacher, 1904, quoting Cuvier and Buffon as authorities) in mammals appears to the author to be erroneous. It has previously been mentioned that no cases of hibernation have been seen in surrounding temperatures much above 20° – 22° C., which must be considered low in comparison with the usual body temperature. The tenrec (*Ctenos ecaudatus*) of Madagascar has often been cited as an animal that hibernates in the warm season but Milne-Edwards (1857–1863) cites evidences that it actually hibernates during the colder season.

Precooling

Koelsch (1925) and others have stated that animals cannot be made to hibernate in the summer by artificial cold and therefore the phenomenon is produced by internal factors only. While the work in this laboratory has shown conclusively that hibernation can be produced any time of the year, it must be admitted that there is less tendency to hibernate and greater mortality in the spring and early summer than in late summer (August), fall and winter. This is doubtless caused in part by internal factors but some evidence has been seen that it may be partly attributed to the previous season of hibernation, the poor conditions and greater excitability of new animals caught just before spring or summer study. It was also found that precooling ground squirrels nightly, as usually happens in the fall in animal quarters before the heat is turned on, caused them to go into hibernation significantly sooner when taken to a cold room than those which had not been precooled (Johnson, 1927, 1930). While precooling probably has facilitated the production of hibernation in the fall by various workers, it should not perhaps be considered a necessary cause in nature. However, intermittent or gradual cooling of the ground in the fall doubtless aids somewhat in preparing the animal for hibernation.

Food

Several authors consider starvation a cause of hibernation (e.g., Mangili, 1807; Hall, 1832; Forel, 1887;

Simpson, 1912; Mann, 1916; Shaw, 1925c), but most of these men and others (e.g. Valentin, 1857) state that little food is eaten before hibernation even if it is present. The latter has not been borne out in ground squirrels in this laboratory. While the presence of food has often not prevented hibernation (Saissy, 1815; Mills, 1892; Wade, 1930) starvation has been found to make ground squirrels hibernate sooner than feeding (Johnson, 1925, 1930). Nineteen experiments in each of which six were fed and six starved and kept in the cold room from 7 to 23 days showed 13 per cent hibernation in the fed groups and 42.4 per cent in the starved groups. The fed groups showed an average of 78.5 per cent days before hibernation while the starved group went into hibernation after an average of only 42 per cent of their days in the refrigerator.

Dry Food

In order to test the theory advanced by Shaw (1925b) and Kashkarov and Lein (1927) that desiccation of vegetation produces aestivation 44 dry feed experiments were run by Kalaboukhov (1929) on 28 *Citellus pygmaeus* Pall. and 2 *Citellus fulvus* Licht. In these experiments there were 11 cases of hibernation in animals given dry feed but none in those given the same food soaked in water. Room temperatures during these experiments were from 12° to 22° C. No torpor occurred at temperatures above 22° C. Kalaboukhov remarks that the lethargy was identical to hibernation, which has also been the author's observation in numerous cases of torpor in the summer. Since no difference was noted no particular mention has been made of summer hibernation in the papers from this laboratory. Returning to Kalaboukhov's statement that no hibernation took place in the animals that had soaked food, it may be remarked that the author has had numerous cases of hibernation in July and August in a room of about 10° C. (a little colder than Kalaboukhov's temperature) among animals given green alfalfa or grass in addition to dry feed. For incidental evidences of this see Johnson (1930, Table I) and Johnson and Hanawalt (1930, Table II). The author has had numerous cases of partial hibernation following drops in room temperature for a night or for a few days in September. These animals hibernated in spite of water kept before them. A *C. t. tridecemlineatus* with a temperature of 31.0° C. in a room of 28.0° C. was only slightly torpid and could walk. Two *C. t. pallidus* at 28.0° and 20.2° C. in a room of 22.0° and 19.0° C. respectively could hardly move when taken up.

Wade (1930) performed some experiments on four *C. t. tridecemlineatus* outdoors and three indoors from July to October in which the animals had access only

to dry feed. His results would not support the conclusions of Kalaboukhov, for Wade's animals did not hibernate, although they lost much in weight. Since Wade's animals were doubtless at a higher temperature and mine were usually at a lower temperature than Kalaboukhov's, his results at temperatures of 12° to 22°C. are not contradicted by Wade's and mine. Furthermore, in a single experiment at 10°-15°C. nine *C. t. pallidus* ground squirrels fed only dry oats went into hibernation in an average of 3.8 days whereas ten fed soaked oats went in at 8.3 days.

Present data would seem to warrant a conclusion that dry food, as compared with moist, may serve as a weak cause of torpor. There is no question, of course, that dry hot weather followed by a drying up of the vegetation tends to drive the ground squirrels (Shaw, 1925b) and prairie dogs (Kashkarov and Lein, 1927) into their burrows, but once there it would seem that the quietness and coolness must aid in the production of torpor, if torpor is common in these animals in the summer.

Light

While many investigators have placed their animals in the dark to hibernate (Mann, 1916), light has not prevented hibernation (Wade, 1930, and others), and no influence on hibernation was found in 19 controlled experiments involving 12 animals each (Johnson, 1925, 1930b). It should be noted that the rolled up position of the animal in sleep and hibernation tends to shut out the light from the eyes even if it is present.

Confined Air

There appears to be no agreement as to the rôle of confined air in the production of hibernation. Mangili (1807) declared that it has no effect, but Bert (1868, 1870) produced a fall in temperature to 12°C. in dormice confined in a bell jar in the cold and Claparède (1905) considered that confined air would lower metabolism, aiding the change from sleep to torpidity. Brown (1847), Wade (1930) and others have mentioned hibernation in open air, but the former considers the lack of oxygen as a cause of hibernation.

In experiments involving 108 animals each in a half gallon can closed tight except for four nail holes about 3.0 mm. in diameter in the lid, the ground squirrels went into hibernation on the average after 19 per cent of their total days in the refrigerator had elapsed, whereas a similar number of controls in open cages hibernated only after 49 per cent of their stay in the refrigerator (Johnson, 1930). That this earlier entrance into hibernation was not produced by the more

limited space of the half-gallon cans was shown by the fact that other controls in similar cans but with the tops highly perforated hibernated practically at the time and to the extent of those in the open cages.

In this connection we may consider Dubois' (1895, 1896) autonarcosis theory, which involves both external and internal conditions. He maintained that an excess of carbon dioxide in the blood is a cause of torpor. Torpid marmots to which he supplied a mixture of 12 per cent oxygen, 43 per cent air and 45 per cent carbon dioxide continued torpid until pure carbon dioxide was added at the beginning of the fifth hour, which caused the respiration rate of 3-5 a minute to double in ten minutes (1895). He concluded that a certain proportion of carbon dioxide would cause torpidity but that a greater proportion of it was responsible for waking. He also found that he could anaesthetize a dog in a mixture of air containing 17.3 per cent carbon dioxide (1901b). Rasmussen (1915, 1916b) found that the carbon dioxide content in the blood of the woodchuck was increased in hibernation, especially in the latter part of this state, but decreased again in waking. He also found that the difference in amounts of gases in the venous and in the arterial blood is greater in the torpid than in the normal animal. In two torpid woodchucks he found no increase in amount of carbon dioxide in the blood, indicating that Dubois' "autonarcosis" theory would not account for all cases of hibernation.

Obesity

Of the internal conditions, fatness has been agreed upon as a cause by practically all who have studied it as a possible factor (e.g., Horvath, 1881; Brown, 1847; Claparède, 1905; Mangili, 1807; Mills, 1892, 1893; Mann, 1916; Johnson, 1930; Wade, 1930). Lack of fatness has probably kept captive animals awake in the winter in some cases. Forel's (1887) dormice, for instance, did not hibernate until they became very fat in May, but from then until August they hibernated at a body temperature of 20°-22°C. A significantly greater amount of hibernation was found by the author in 38 heavy ground squirrels than in 118 light animals (Johnson, 1930) and the greater tendency of fat animals to hibernate has been observed in many animals in other experiments. Sometimes it would appear that very thin animals went into hibernation sooner than those of medium weight but closer study revealed the fact that such animals very frequently died after two or three days in torpor, so that their hibernation is not normal. Probably deaths reported by others as occurring when animals have been cooled in the summer have been due to thinness of the animals, and possibly also to the sudden transfer from hot to cold atmospheres.

Loss of Body Moisture

Loss of body water may be considered a possible internal cause, although it may be caused in turn by a dry food diet, which has already been found slightly conducive to hibernation. Since desiccation has been found to favor hibernation in the potato beetle (Tower, 1906; Breitenbecher, 1918; Fink, 1925) and also to produce cold hardiness in insects (Bodine, 1923; Payne, 1927) it is interesting to note that Dubois (1895, 1909) found that the blood of torpid marmots was somewhat desiccated. Rasmussen (1915, 1916c) found an increase of 5 per cent in erythrocytes in hibernation and a 20 per cent decrease after the woodchucks had eaten and drunk, indicating a tendency to desiccation in hibernation. It is concluded by Gorer (1930), however, that the water balance is not uniform in hibernating mammals.

Hypofunction of the Thyroid Gland

Histological work on the thyroid of ground squirrels, *C. t. tridecemlineatus*, (Mann, 1916; and Peiser, 1906, according to Gorer, 1930) led to no evidence of a relationship to hibernation, but did show a flattening of the cells and a great diminishing of colloid in the fall. Adler (1920a) found histological changes in thyroids of bats and hedgehogs that indicated excessive secretion of colloid just after waking in the spring and this was later confirmed by Coninx-Girardet (1927). Subcutaneous injections of extracts of thyroid and also of thymus and suprarenals were found usually to produce waking in the hedgehog by Adler (1920a, 1926). From other experiments in which the heat regulating center had been removed and the sympathetic nervous system deadened with ergotoxin he concluded that these substances produced waking by increasing oxidative processes at the periphery and not wholly by action on the heat regulating center or on the sympathetic nervous system (Adler, 1920b, 1926). Schenk (1922) also found the same extracts produced a rise in metabolism and sometimes a waking in torpid hedgehogs. Zondek (1924), however, produced waking not only with Adler's extracts but also with others including physiological salt solution of a temperature of 8°C. or more above the rectal temperature of the animal and concluded that the warmth and not the specific nature of Adler's extracts produced waking.

Intra-peritoneal injections of very large doses of thyroxin (31 to 52 times the human dose considering comparative body weights) in 66 *C. t. pallidus* and feeding of thyroid substances to 23 produced no inhibition of hibernation over that of the controls (Johnson and Hanawalt, 1926, 1930). From these experiments it appears that the thyroid does not pre-

vent hibernation and that the increased activity of the gland in the spring, shown by Adler (1920a) and Coninx-Girardet (1927) is not the cause of waking but accompanies it, possibly as a result.

Adrenal Glands

Adler's (1920a) work indicating an inhibitory effect of an adrenal extract as well as thyroid and thymus extracts and Zondek's (1924) refutation of it have already been mentioned. Enlargement of the adrenals of *C. t. tridecemlineatus* in the spring was reported by Mann (1916), but little change except an enlargement of the blood vessels was found in these glands in the winter (Coninx-Girardet, 1927). Britton (1928) has shown that in artificially cooled cats the presence of the adrenals is necessary for spontaneous awakening from this condition of torpor and suggests that waking from hibernation is produced by increased "sympatico-adrenal" activities, whereas entrance into hibernation is caused by decreased activity.

The Pituitary Gland

Gemelli (1906) observed no change in the posterior lobe but in the anterior he found a great decrease in number of "cyanophile" cells in hibernation in the marmot. Cushing and Goetsch (1915) observed drowsiness and a lowering of temperature, respiration and heart beat in humans with diseased pituitaries. They also found reduction in size of the ductless glands, especially of the anterior pituitary, in hibernating marmots and a production of fatness and drowsiness in a young hypophysectomized dog. Mann (1916) found no constant change in the pituitary associated with seasons in the ground squirrel. Rasmussen (1921) found no changes from fall to winter in woodchucks but found indications of increased activity in the spring. Coninx-Girardet (1927) found an increase in number of basophile cells in the woodchucks in the spring including the breeding season, which also indicated increased activity of the pituitary at that time. In the winter decreased activity was indicated by a reduction in number of basophile cells and by a more open grouping of the cells of the pituitary.

While the histological appearance of the anterior pituitary indicates renewed activity in the spring it should be noted that this might be a result and not a cause of waking and only physiological experiments can give conclusive evidence. Experiments in this laboratory with a weak extract by B. R. Coonfield and the author showed no effect on hibernation. More recently a stronger alkaline extract has shown some inhibitory action and subcutaneous injection of cut

pieces of the pituitary into 20 ground squirrels has shown marked inhibitory effects on entrance into hibernation.

No evidence has been produced which indicates that the posterior pituitary has any influence on hibernation; on the contrary, the injection of pituitrin by Johnson and Hanawalt (1926, 1930) gives definite evidence that it has neither an inhibitory nor a causative action on hibernation.

Gonads

Gonadal enlargement in hibernating forms in the spring has been found by Mann (1916), Drips (1919), Rasmussen (1917, 1918), Shaw (1926) and Johnson (1930). Mann showed that castration did not prevent hibernation in *C. r. tridecemlineatus*. That gonadal activity tends to prevent hibernation in the spring but not at other times of the year has been shown by Johnson (1927, 1930) in *C. r. pallidus*, for castrated animals hibernated to a significantly greater extent than did normal animals during the breeding season. It was also recognized that this activity is probably caused by increased secretion of the anterior pituitary.

Other Possible Causes Investigated

Removal of the spleen was found to show no effect on hibernation by Mann and Drips (1917), although they found the vessels much congested. Extracts of the thymus used by Adler (1920a) produced waking from hibernation, but this work was questioned by Zondek (1924), and other work seems to raise the question whether this structure is an endocrine organ. Structural differences between hibernators and other

animals were sought by Mangili (1807), who considered that the arterial blood supply to the brain was small in hibernating forms, and by Saissy (1815), who stressed the large blood vessels of the thorax and abdomen, small peripheral vessels, large nerves to the head, and limited blood supply to the brain as characteristic features in hibernating forms. While many authors have noted the lack of peripheral bleeding when a hibernating animal is cut and have seen the congestion in the chief blood vessels, it would not seem that these can have a causative relation to hibernation.

Injection of insulin sufficient to produce hypoglycemia caused woodchucks, dogs and cats to pass temporarily into a state of torpor (Cassidy, Dworkin and Finney, 1925a, b; Dworkin and Finney, 1927), in which the respiratory quotient fell in the dogs as if they were in true hibernation (Finney, Dworkin and Cassidy, 1927). Injection of adrenalin and pituitrin brought back the shivering reflexes in partly torpid animals that had ceased to shiver (Cassidy, Dworkin and Finney, 1926). Whether these observations reveal any internal causes of hibernation it is difficult to say. It would be interesting to know whether the blood sugar level of an animal that falls into hibernation very readily is different from that of one that shows great resistance to hibernation in a cold room.

The inhibiting effect on hibernation of external stimuli has long been recognized. Thus Dubois (1896) found that the taking of temperatures of the marmot tended to shorten its hibernating period and Brown (1847) found that excitability kept animals awake.

LIST OF LITERATURE

- ADLER, L. 1920a. Schilddrüse und Wärmeregulation (Untersuchungen an Winterschläfern). Arch. exper. Path., 86: 159-224.
- . 1920b. Über den Angriffspunkt der Blutdrüsenhormone bei der Wärmeregulation. Weitere Untersuchungen an Winterschläfern. Arch. exper. Path., 87: 406-423.
- . 1926. Der Winterschlaf. Handbuch der Normalen und Pathologischen Physiologie, 17: 105-133.
- ANTHONY, H. E. 1928. Field Book of North American Mammals. Putnam, New York.
- BALBY, V. 1926. Hibernation good for mankind too. New York Times, July 4, p. 6.
- . 1928. Animal Life of the Carlsbad Cavern. Williams and Wilkins, Baltimore.
- BALDWIN, F. M. 1925. Body temperature changes in turtles and their physiological interpretations. Amer. Jour. Physiol., 72: 210-211.
- BARKOW, H. C. L. 1846. Der Winterschlaf nach seinen Erscheinungen im Thierreich. Hirschwald, Berlin.
- BAYLISS, W. M. 1918. Principles of General Physiology. Longmans, London.
- BERT, P. 1868. Hibernation artificielle des lérots dans une atmosphère lentement appauvrie en oxygène. Comp. rend. Soc. biol., Sér. 4, 5: 13.
- . 1870. Leçons sur la physiologie comparée de la respiration. Paris.
- BIERENS DE HAAN, J. A. 1922. Die Körpertemperatur junger Wanderratten (*Mus decumanus*) und ihre Beeinflussung durch die Temperatur der Aussenwelt. Archiv f. Entw.-Mech. der Organismen, 50: 1-12.
- BLANCHARD, R. 1903. Expériences et observations sur la marmotte en hibernation. Comp. rend. Soc. biol., 55: 734-741; 1120-1126.

- BODINE, S. H. 1923. Hibernation in Orthoptera. I. Physiological changes during hibernation in certain Orthoptera. Jour. Exp. Zool., 37: 457-476.
- BREITENBECHER, J. K. 1918. The relation of water to the behavior of the potato beetle in a desert. Carnegie Inst. Wash., Pub. No. 263: 341-384.
- BRITTON, S. W. 1922. Effects of lowering the temperature of homoiothermic animals. Quart. Jour. Exp. Physiol., 13: 55-68.
- . 1928. Studies on the conditions of activity in endocrine glands. XXII. Adrenin secretion on exposure to cold, together with a possible explanation of hibernation. Amer. Jour. Physiol., 84: 119-131.
- BROWN, P. A. 1847. An Attempt to Discover Some of the Laws Which Govern Animal Torpidity and Hibernation. Philadelphia.
- BUCHANAN, F. 1911. Dissociation of auricles and ventricles in hibernating dormice. Proc. Physiol. Soc. (Jour. Physiol., 42: xix-xx).
- BURNETT, W. L. 1914. The striped ground squirrels of Colorado. Office of State Entomologist, Fort Collins, Colo., Circ. 14.
- BUSE, K. 1885. Hibernation. Nature, 31: 316-317 and 482.
- CARLISLE, A. 1805. The Croonian lecture on muscular motion. Phil. Trans. (Lond.), 95: 1-30.
- CASSIDY, G. J., DWORKIN, S., and FINNEY, W. H. 1925a. The rate of action of insulin in artificially cooled mammals. Amer. Jour. Physiol., 73: 413-416.
- . 1925b. Insulin and the mechanism of hibernation. Amer. Jour. Physiol., 73: 416-428.
- . 1926. The effect of various sugars (and of adrenalin and pituitrin) in restoring the shivering reflex. Amer. Jour. Physiol., 77: 211-218.
- CLAPARÈDE, E. 1905. Théorie biologique du sommeil. Arch. d. Psychol., 4: 245-349.
- CLEGHORN, A. 1910. Natural history and physiology of hibernation. Pop. Sci. Mo., 77: 356-364.
- CONINX-GIRARDET, B. 1927. Beiträge zur Kenntnis innersekretorischer Organe des Murmeltieres (*Arctomys marmota* L.) und ihrer Beziehungen zum Problem des Winterschlafes. Acta Zoologica, 8: 161-224.
- CORY, C. E. 1912. The mammals of Illinois and Wisconsin. Field Mus. of Nat. Hist. Pub., Zool. Ser., 11.
- CUSHING, H., and GOETSCH, E. 1915. Hibernation and the pituitary body. Jour. Exp. Med., 22: 25-47.
- DELSAUX, E. 1887. Sur la respiration des Chauves-Souris pendant leur sommeil hibernant. Arch. de Biol., 7: 207-215.
- DRIPS, D. 1919. Studies of the ovary of the spermo-phil. Amer. Jour. Anat., 25: 117-184.
- DUBOIS, R. 1895. (Three short articles on autonarcosis). Comp. rend. Soc. biol., 47: 149-151; 814-815; 830-831.
- . 1896. Étude sur le mécanisme de la thermogénèse et du sommeil chez les mammifères. Physiologie comparée de la marmotte. Annales de l'Université de Lyon. Paris.
- . 1901a. Le centre du sommeil. Comp. rend. Soc. biol., 53: 229-230.
- . 1901b. Sommeil naturel par autonarcose carbonique provoqué expérimentalement. Comp. rend. Soc. biol., 53: 231-232.
- DWORKIN, S., and FINNEY, W. H. 1927. Artificial hibernation in the woodchuck (*Arctomys monax*). Amer. Jour. Physiol., 80: 75-81.
- FINK, D. E. 1925. Physiological studies on hibernation in the potato beetle, *Leptinotarsa decemlineata* Say. Biol. Bull., 49: 381-406.
- FINNEY, W. H., DWORKIN, S., and CASSIDY, G. J. 1927. The effects of lowered body temperatures and of insulin on the respiratory quotients of dogs. Amer. Jour. Physiol., 80: 301-310.
- FITZPATRICK, F. L. 1925. The ecology and economic status of *Citellus tridecemlineatus*. University of Iowa Studies in Nat. Hist., 11: 1-40.
- FOREL, A. 1887. Observations sur le sommeil du loir (*Myoxis glis*). Revue de l'hypnot. exp., 1: 318-319. (Also in Centralbl. f. Physiol., 1: 208-209).
- GEMELLI, A. 1906. Su l'ipofisi delle marmotte durante il letargo e nella stagione estiva. Archivio per le Scienze Mediche, 30: 341-349.
- GORER, P. A. 1930. The physiology of hibernation. Biol. Rev. (Camb.), 5: 213-230.
- HAHN, W. L. 1908. Some habits and sensory adaptations of cave-inhabiting bats. Biol. Bull., 15: 135-193.
- . 1914. Hibernation of certain animals. Pop. Sci. Mo., 84: 147-157.
- HALL, M. 1832. On hibernation. Phil. Trans. (Lond.), Pt. I: 335-360.
- HATT, R. T. 1927. Notes on the ground-squirrel, *Callospermophilus*. Occas. papers, Mus. Zool., Univ. of Michigan, 185: 1-22.
- HORVATH, A. 1872a. Zur Physiologie der tierischen Wärme. Zentralbl. f. med. Wissensch., pp. 706-708; 721-724; 734-739.
- . 1872b. Zur Lehre vom Winterschlaf. Zentralbl. f. med. Wissensch., pp. 865-866.
- . 1874. Zur Abkühlung der Warmblüter. Pflüger's Archiv f. Physiol., 12: 278-282.
- . 1878. Beitrag zur Lehre über den Winterschlaf. Verh. d. Phys.-Med., N. F., 12: 139-198.

- HORVATH, A. 1880. Ueber die Respiration des Winterschläfer. Verh. d. Phys.-Med., N. F., 14: 55-120; 15: 177-186.
- . 1881. Einfluss verschiedener Temperaturen auf die Winterschläfer. Verhandl. d. Phys.-Med., N. F., 15: 187-219.
- HOWELL, A. H. 1915. Revision of the American marmots. N. Am. Fauna, No. 37.
- HOY, P. R. 1875. On hibernation as exhibited in the striped gopher. Proc. Amer. Assoc. Adv. Sci., 24: 148-150.
- HULK, A. H. 1885. Human hibernation. Nature, 31: 361.
- HUNTER, J. 1837. Experiments and observations on animals with respect to the power of producing heat. The Works of John Hunter (London), 4: 131-155.
- JOHNSON, G. E. 1917. The habits of the thirteen-lined ground squirrel. Quart. Jour. Univ. N. Dakota, 7: 261-271.
- . 1925. Some conditions affecting the hibernation of the thirteen-lined ground squirrel. Anat. Rec., 31: 337.
- . 1927. The influence of precooling, castration, and body weight on the production of hibernation of *Citellus tridecemlineatus* (Mitchill). Anat. Rec., 37: 125.
- . 1928. Hibernation of the thirteen-lined ground squirrel, *Citellus tridecemlineatus* (Mitchill). I. A comparison of the normal and hibernating states. Jour. Exp. Zool., 50: 15-30.
- . 1929a. Hibernation, etc., II. The general process of waking from hibernation. Am. Nat., 63: 171-180.
- . 1929b. Hibernation, etc., III. The rise in respiration, heart beat and temperature in waking from hibernation. Biol. Bull., 57: 107-129.
- . 1929c. The fall in temperature in ground squirrels going into a state of hibernation. Anat. Rec., 44: 199.
- . 1930. Hibernation, etc., V. Food, light, confined air, pre-cooling, castration and fatness in relation to production of hibernation. Biol. Bull., 59: 114-127.
- JOHNSON, G. E., and HANAWALT, V. B. 1926. The influence of thyroxin and of pituitrin on the hibernation of *Citellus tridecemlineatus pallidus* Allen. Anat. Rec., 34: 137.
- . 1930. Hibernation, etc., IV. Influence of thyroxin, pituitrin and desiccated thymus and thyroid on hibernation. Am. Nat., 64: 272-284.
- KALABOUKHOV, N. I. 1929. Aestivation of the ground squirrel. Trans. Lab. Exp. Biol. Zoopark of Moscow, 5: 163-176.
- KASHKAROV, D., and LEIN, L. 1927. The yellow ground squirrel of Turkestan, *Cynomys fulvus oxianus* Thomas. Ecology, 8: 63-72.
- KOELSCH, A. 1925. Der Mechanismus des Winterschlafs. Kosmos, Heft 1, (Jan.): 14-17.
- MANGILI, M. 1807. Ueber den Winterschlaf der Thiere. Arch. f. d. Physiol. (Reil), 8: 427-448. A similar article in Ann. d. Mus. hist. nat., 9: 106-117; 10: 434-465, (1807).
- MANN, F. C. 1916. The ductless glands and hibernation. Amer. Jour. Physiol., 41: 173-188.
- MANN, F. C., and DRIES, D. 1917. The spleen during hibernation. Jour. Exp. Zool., 23: 277-285.
- MARES, M. F. 1892. Expériences sur l'hibernation des Mammifères. Comp. rend. Soc. biol., 44: 313-320.
- MARTIN, C. J. 1901. Thermal adjustments and respiratory exchange in Monotremes and Marsupials. Proc. Roy. Soc. London, 68: 352-353.
- MERRIAM, C. H. 1901. The prairie dog of the great plains. U. S. Dept. Agr. Yearbook, pp. 255-270.
- MERZBACHER, L. 1903a. Untersuchungen über die Function des Centralnervensystems der Fledermaus. Arch. f. d. ges. Physiol., 96: 572-600.
- . 1903b. Untersuchungen an winterschlafenden Fledermäusen. I. Mittheilung. Das Verhalten des Centralnervensystems in Winterschlaf und während des Erwachens an demselben. Arch. f. d. ges. Physiol., 97: 569-577.
- . 1904. Allgemeine Physiologie des Winterschlafes. Ergebn. d. Physiol., 3 (Abt. 2): 214-258.
- MILLS, W. 1892. Hibernation and allied states in animals. Trans. Roy. Soc. Canada, Sec. IV: 49-51. A part also in Trans. Pan-Amer. Med. Congr. Wash., 1893, Pt. II: 1274.
- MILNE-EDWARDS, H. 1857-63. Leçons sur la Physiologie (Paris), 2: 490-491; 2: 519-525; 4: 76; 8: 58-68.
- MONTI, R., and MONTI, A. 1900. Osservazioni sulle marmotte ibernanti. Reale Inst. Lombardo di sci. e let. Rend. Ser. II, 33: 372-381.
- MURRAY, J. 1826. On the torpidity of the tortoise and dormouse. Edinburgh Jour. Sci., 4: 317-322.
- PAYNE, N. M. 1927. Freezing and survival of insects at low temperatures. Jour. Morph., 43: 521-546.
- PMBREY, M. S. 1895. The effect of variations in external temperature upon the output of carbonic acid and the temperature of young animals. Jour. Physiol., 18: 363-379.
- . 1898. Animal heat. Textbook of Physiology (Edited by Schafer), 1: 785-867.

- PEMBREY, M. S. 1901. Observations upon the respiration and temperature of the marmot. *Jour. Physiol.*, 27: 66-84.
- . 1903. Further observations upon the respiratory exchange and temperature of hibernating mammals. *Jour. Physiol.*, 29: 195-212.
- PEMBREY, M. S., and WHITE, W. H. 1896. The regulation of temperature in hibernating animals. *Jour. Physiol.*, 19: 477-495.
- PEMBREY, M. S., and PITTS, A. G. 1899. The relation between the internal temperature and the respiratory movements of hibernating animals. *Jour. Physiol.*, 24: 305-316.
- POLIMANTI, O. 1912. *Il Letargo*. Roma.
- PRATT, H. S. 1923. *Vertebrate Animals of the United States*. Blakistons, Philadelphia.
- QUINCKE, H. 1881. Ueber die Wärme-regulation beim Murmelthier. *Arch. f. exp. Path.*, 15: 1-21.
- RASMUSSEN, A. T. 1915. The oxygen and carbon dioxide content of the blood during hibernation in the woodchuck (*Marmota monax*). *Amer. Jour. Physiol.*, 39: 20-30.
- . 1916a. Theories of hibernation. *Am. Nat.*, 50: 609-625.
- . 1916b. A further study of the blood gases during hibernation in the woodchuck (*Marmota monax*). The respiratory capacity of the blood. *Amer. Jour. Physiol.*, 41: 162-172.
- . 1916c. The corpuscles, hemoglobin content and specific gravity of the blood during hibernation in the woodchuck (*Marmota monax*). *Amer. Jour. Physiol.*, 41: 464-482.
- . 1917. Seasonal changes in the interstitial cells of the testis in the woodchuck (*Marmota monax*). *Amer. Jour. Anat.*, 22: 475-509.
- . 1918. Cyclic changes in the interstitial cells of the ovary and testis in the woodchuck (*Marmota monax*). *Endocrin.*, 2: 353-404.
- . 1921. The hypophysis cerebri of the woodchuck (*Marmota monax*) with special reference to hibernation and inanition. *Endocrin.*, 5: 33-66.
- . 1923. The so-called hibernating gland. *Jour. Morph.*, 38: 147-205.
- REEVE, H. 1809. *An Essay on the Torpidity of Animals*. London.
- SAISSY, J. A. 1811. Observations sur quelques mammifères hybernans. *Mém. Acad. d. Sci. d. Turin*, pt. 2: 1-21.
- . 1815. Untersuchungen über die Natur der winterschlafenden Säugethiere. *Arch. f. d. Physiol.*, 12: 293-369.
- SCHENK, P. 1922. Ueber den Winterschlaf und seine Beeinflussung durch die Extrakte innersekretorischer Drüsen. *Arch. ges. Physiol.*, 197: 66-69.
- SEMPER, K. 1881. *Animal Life as Affected by the Natural Conditions of Existence*. Appleton, New York.
- SETON, E. T. 1928. *Lives of Game Animals*, Vol. 2. Doubleday, Page and Co., Garden City, N. Y.
- SHAW, W. T. 1921. Moisture and altitude as factors in determining the seasonal activities of the Townsend ground squirrel in Washington. *Ecology*, 2: 189-192.
- . 1925a. The hibernation of the Columbian ground squirrel. *Canad. Field Nat.*, 39: 56-61 and 79-82.
- . 1925b. Observations on the hibernation of ground squirrels. *Jour. Agr. Res.*, 31: 761-769.
- . 1925c. Duration of the aestivation and hibernation of the Columbian ground squirrel (*Citellus columbianus*) and sex relation to the same. *Ecology*, 6: 75-81.
- SHELDON, E. F. 1924. The so-called hibernating gland in mammals: A form of adipose tissue. *Anat. Rec.*, 28: 331-347.
- SIMPSON, S. 1911-12. The relation of external temperature to hibernation. *Amer. Jour. Physiol.*, 29: xii. Also in *Proc. Soc. Exp. Biol. and Med.*, 10: 180-181 (1913).
- . 1912. The food factor in hibernation. *Proc. Soc. Exp. Biol. and Med.*, 9: 92.
- SPALLANZANI, L. 1803. *Mémoires sur la respiration*, traduits en Français, par Jean Senebier, Genève. pp. 106-117.
- SUMNER, F. B. 1913. The effects of atmospheric temperature upon the body temperature of mice. *Jour. Exp. Zool.*, 15: 315-377.
- STOCKARD, A. H. 1930. Observations on the seasonal activities of the white-tailed prairie dog, *Cynomys leucurus*. *Papers, Mich. Acad. Sci., Arts and Let.*, 11: 471-479.
- SWENK, M. H. 1915. The prairie dog and its control. *Bul. 154, Neb. Agr. Exp. Sta.*
- TAIT, J., and BRITTON, S. W. 1923. *Quart. Jour. Exp. Physiol.*, Sup. Vol. 226.
- TOWER, W. L. 1906. An investigation of evolution in Chrysomelid beetles of the genus *Leptinotarsa*. *Carnegie Inst. Wash. Pub. No. 48*: 1-320.
- VALENTIN, G. 1857. Beiträge zur Kenntnis des Winterschlafes der Murmelthiere. *Unters. zur Naturl. des Menschen und der Thiere*, von Jac. Moleschott, 1: 206-258 and 2: 1-55. (A series of 27 articles, 1857-1888).
- WADE, O. 1930. The behavior of certain spermo-philus with special reference to aestivation and hibernation. *Jour. Mammal.*, 11: 160-188.
- WILLIAMS, S. R. 1909. On hibernation in the raccoon. *Ohio Naturalist*, 9: 495-496.
- ZONDEK, B. 1924. Untersuchungen über den Winterschlaf. *Klin. Wchnschr.*, Heft 34, 3: 1529-1530.

THE THREE TYPES OF MORTALITY CURVE

By ISTVÁN SZABÓ

Kaposvár, Hungary

THE death-rates of different organisms are compared by Pearl (1) by plotting the number of survivors on arithlog paper. In this, as our figure shows (Fig. 1), the abscissal scale is divided arithmetically, and the scale of ordinates geometrically. The abscissa indicates age, but Pearl subdivides the life span of each organism into centiles, and thus he compares the different life spans of different organisms on a single graph. The ordinate signifies the number of survivors. It shows, therefore, how many individuals out of 1,000 living at age 0 are alive at successive ages, expressed as centiles of the life span. On reaching the one-hundredth centile, the last individual dies and the curve touches the abscissal axis. Now Pearl states that, theoretically, three types of the curve can be imagined. The first is the rectangular type, referring to individuals who live for about the same period and die at the same age. This type is approximated by the life curve of *Proales decipiens*, of present-day man, and of wild *Drosophila*.

The second type is the diagonal, which is represented on arithlog paper by a straight line; the death-rate is constant from the beginning of life to its end. This type is approximated by the life curve of vestigial *Drosophila*.

In the third type there is a large initial death-rate; the curve declines sharply at the beginning of life, and then runs almost horizontally until the end of the life span. Pearl reports in his work of 1928 that he

has never actually happened to observe this type of life curve, which may be imagined theoretically.

In this short paper I take the liberty of pointing out that the mortality curve of forest trees is an example of this third type, which I should like to name the hyperbolic type, as it is hyperbola-shaped.

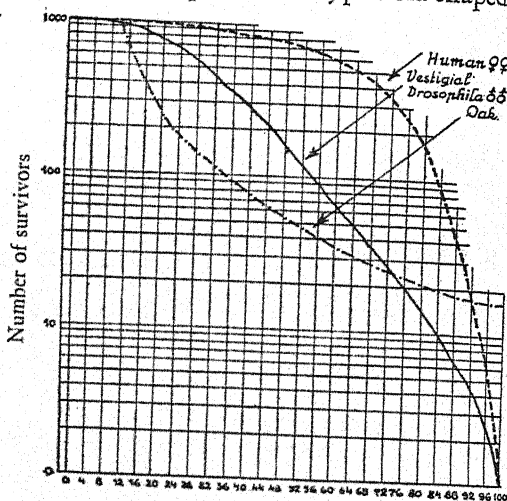


FIG. 1. SURVIVORSHIP CURVES OF MAN, OF VESTIGIAL DROSOPHILA, AND OF THE OAK

The first two are after Pearl, *The Rate of Living*, A. A. Knopf, N. Y., p. 43; the third is based on Fekete's data.

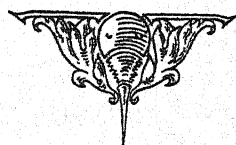
In Figure 1 are shown the life curves of man and vestigial *Drosophila* (from Pearl, p. 38), together with that of the oak, based on the data of Fekete. There are no data for the latter under twenty years or above 200 years. However, the observed part of the curve has a form corresponding to Pearl's theoretical third type of life curve.

According to Pearl, the curves should

start at biologically equivalent ages. He death-rate is then a minimum. In the therefore begins the *Drosophila* curve at hyperbolic type this condition can not be the first day of imaginal life and the human fulfilled, since the death-rate shows no curve at the twelfth year of life, as the minimum near the beginning of life.

LIST OF LITERATURE

1. PEARL, R. The Rate of Living. New York. 1928.
2. FEKETE, L. Erdőmérnöki táblázatok. Sopron. 1916. pp. 56-57.





NEW BIOLOGICAL BOOKS

The aim of this department is to give the reader brief indications of the character, the content, and the value of new books in the various fields of biology. In addition there will frequently appear one longer critical review of a book of special significance. Authors and publishers of biological books should bear in mind that THE QUARTERLY REVIEW OF BIOLOGY can notice in this department only such books as come to the office of the editor. The absence of a book, therefore, from the following and subsequent lists only means that we have not received it. All material for notice in this department should be addressed to Dr. Raymond Pearl, Editor of THE QUARTERLY REVIEW OF BIOLOGY, 1901 East Madison Street, Baltimore, Maryland, U. S. A.

BRIEF NOTICES

EVOLUTION

COPE: MASTER NATURALIST. *The Life and Letters of Edward Drinker Cope with a Bibliography of His Writings Classified by Subject. A Study of the Pioneer and Foundation Periods of Vertebrate Palaeontology in America.*

By Henry Fairfield Osborn with the Co-operation of Helen A. Warren, and Citations from the Writings of George Brown Goode, Theodore Gill, Persifor Frazer, Henry Fairfield Osborn, William Berryman Scott, William King Gregory, William Diller Matthew.

Princeton University Press

\$5.00 6 x 9 $\frac{1}{4}$; xvi + 740 Princeton

In this book Professor Osborn has made an outstanding addition to his already long and noteworthy list of biographical writings. Edward Drinker Cope was in some ways the most romantic figure in the history of American science. Undoubtedly a genius, he had a colossal capacity for work coupled with great intellectual brilliancy and originality. These qualities in themselves were enough to cause a plenitude of difficulties in an American academic career. But over and beyond the troubles which were caused by these elements in his own make-up Cope

suffered the misfortune of arousing first the jealousy and then the bitter enmity of a rich and academically powerful paleontologist, whose complex character cannot be accurately or adequately described in a farm and garden magazine such as this, even though the National Academy of Sciences did see fit to make him its president. It must suffice to say that the later part of Cope's life was full of troubles and difficulties. This is, of course, a familiar and ever-recurring story in the history of science, and, indeed, in the history of mankind generally. Like many geniuses, and not a few other folk, Cope was in some respects a foolish fellow. This helped to his undoing. But happily time has already given him a fairer and sweeter fame than lingers about the memory of some of those who opposed him and who got most of the breaks during life.

The great value of this book primarily arises from the fact that Cope's daughter made available to Professor Osborn all of her father's letters and papers. With masterly skill these have been put in order, edited, and amplified so to tell effectively, clearly, and honestly the story of a great life. This volume, coupled with the

National Academy biographical memoir on Cope by the same author, together make a fitting and adequate record. Biologists will always be grateful to Professor Osborn for this splendid piece of work.



LECTURES ON DARWINISM

By *Arthur Willey* *Richard G. Badger*
\$2.00 $5\frac{1}{4} \times 7\frac{3}{4}$; 198 Boston

The title of this book is a trifle misleading, in that relatively little space is actually devoted to Darwinism, in the sense of natural selection. The book, however, is reminiscent of the Darwinian style in its constant preoccupation with illustrations from concrete biological observations. The author's concluding paragraph runs:

If we can see no particular future advances in store for natural selection it is because one cannot help feeling that its work is mainly accomplished, both as a factor and as a theory. It cannot contribute any more than it has done already to solve the riddle of human life nor to improve the status of wild life. As a doctrine it is an achievement of the nineteenth century, as an aid to evolution it is a monument of the past and has hardly more direct bearing upon twentieth century life than has Cleopatra's Needle. It explains the origin of species up to a certain point but accounts in still larger measure for the relative constancy of established species. The apparent fixity of species could easily be mistaken for absolute fixity and this erroneous idea persisted up to the period which witnessed the simultaneous publication of the independent works of C. Darwin and A. R. Wallace. Its worst fault is that it cannot be verified experimentally, while there are many other biological problems which are amenable to experimentation. From being a hotly contested issue it has become a hollow truth, like the bowl of the Eastern Sage, chiefly valuable because of its emptiness.



THE PROBLEMS OF EVOLUTION

By *Arthur W. Lindsey* *The Macmillan Co.*
\$2.00 $5 \times 7\frac{1}{4}$; xiii + 236 New York

An attempt at a restatement of the problem, more particularly with reference to

the old question of heredity and environment. The author emphasizes the position (which seems almost self-evident to us) that the actual characters of an organism are necessarily the result of the interaction of both factors. He believes that there is still room for experimental attempts to show that evolutionary changes can be produced under the stimulus of changed environment.



GENETICS

SELBSTSTERILITÄT UND KREUZUNGSSTERILITÄT IM PFLANZENREICH UND TIERREICH

By *Friedrich Brieger* *Julius Springer*
33.80 marks (bound) *Berlin*
32 marks (paper) $5\frac{5}{8} \times 8\frac{1}{2}$; xi + 395

Besides the cases of true sterility, in which no functional gametes are developed, there are numerous cases, especially in plants, when gametes which are fertile in certain combinations fail in others to combine into a zygote. To this phenomenon, which may prevent on the one hand self-fertilization or on the other hand crossing, Dr. Brieger gives the name parasterility. There are various ways in which this may happen. In plants the pollen may be prevented from reaching the stigma, or having reached it, may not sprout normally; the pollen tubes may be retarded in their growth through the tissues of the style, or having reached the ovary, may not be attracted to the ovules; or finally, the pollen nucleus may not unite with the egg nucleus. In all cases there is a disturbance of the normal relations between the male and female elements. There is no relation between the systematic position of a species and the sterility phenomena which it displays.

Dr. Brieger is sceptical of the teleologi-

cal character of self-parasterility, since it shields unfavorable recessive characters from the action of natural selection.



RACIAL INVESTIGATIONS. X. *The Atlantic Cod (Gadus callarias L.) and Local Races of the Same. Comptes Rendus des Travaux du Laboratoire Carlsberg. 18^{me} Volume No. 6*

By *Johs. Schmidt* Laboratoire Carlsberg
5 Kr. Copenhagen

6 x 9½; 72 + 10 plates (paper)

An investigation of variation in the cod, based on about 20,000 specimens from 114 stations, covering the greater part of the region of occurrence of the species in the Atlantic. The characters studied were the number of vertebrae and the number of rays in the second dorsal fin. It is found that there are considerable local variations in both characters. There is a distinct correlation between temperature and the variables studied in the open sea stations, a lower temperature being associated with increases in number of vertebrae and dorsal fin rays. There is no direct evidence as to the mechanism of the association.



DIE SEXUELLEN ZWISCHENSTUFEN

By *Richard Goldschmidt* Julius Springer
45 marks (paper) Berlin
46.40 marks (bound)

5½ x 8¼; x + 528

This exhaustive study of intersexuality and gynandromorphism will be of great interest and importance to workers in genetics. The author presents his own work with *Lymantria* in detail, as being the most completely understood case; and then summarizes the results obtained with other forms, and attempts to bring them in line with his theory of the physiological action of the genes.

THE PRACTICAL DOG BOOK. *With Chapters on the Authentic History of All Varieties Hitherto Unpublished, and a Veterinary Guide and Dosage Section, and Information on Advertising and on Exporting to All Parts of the World. A Comprehensive Work Dealing with the Buying, Selling, Breeding, Showing, Care, and Feeding of the Dog.*

By *Edward C. Ash* The Derrydale Press
\$7.50 6½ x 9½; xxxii + 343 New York

This book contains histories of all breeds, a complete guide on feeding, breeding, and showing, and other information. To dog lovers of an antiquarian turn of mind the many illustrations from early books will be of interest. A useful reference work for the genetics library.



GENERAL BIOLOGY

A BIOLOGICAL STUDY OF THE OFFSHORE WATERS OF CHESAPEAKE BAY. *U. S. Department of Commerce, Bureau of Fisheries Document No. 1091.*

By *R. P. Cowles*

U. S. Government Printing Office
30 cents 7½ x 11; 104 (paper) Washington

Chesapeake presents many interesting biological problems. In shape it is a long, narrow body of water (160 nautical miles in length, 5 to 20 in width) extending almost directly north and south in the states of Maryland and Virginia. A fairly narrow opening (10 miles in width) at its southern end gives outlet to the Atlantic Ocean. Two large rivers, the Susquehanna and the Potomac, and numerous smaller rivers, empty their waters into the bay. In addition there are numerous bays, sounds, and small inlets. Although in general the bay is rather shallow, 30 or 40 feet being about the average for deep water, there are far deeper areas along the eastern shore. While there are no very strong currents in the water yet there is an

ever changing condition due to the inflow of many rivers, the ebb and flow of the tide, eddies, and currents of water moving in more or less opposite directions at the surface and bottom in the same locality. In addition there are the seasonal changes in temperature, rainfall, and strong winds.

The survey, which covers a period of several years, has already yielded much of importance. Thirty widely distributed areas have been visited at intervals. Collection and identification of the plants and animals have been made to ascertain their distribution and abundance. Environmental conditions have been recorded. Studies in salinity, temperature and plankton content will, as the survey continues, yield much needed information on the laws which govern the migration of fishes and crabs in the bay. It is expected that knowledge of the normal conditions of the bay will be of great aid in ascertaining what unusual changes have occurred during those years when there has been a great mortality of fishes, oysters, crabs and clams, food products which are a great economic asset to the two states.

The paper includes charts exhibiting the changes of salinity and temperature in different areas and seasons, and a lengthy bibliography.



A YEAR ON THE GREAT BARRIER REEF. *The Story of Corals and of the Greatest of Their Creations.*

By C. M. Yonge G. P. Putnam's Sons
\$6.00 New York and London

6 $\frac{1}{4}$ x 9 $\frac{5}{8}$; xx + 246

This delightful book is a by-product of the Great Barrier Reef Expedition of 1928-29. The party under Dr. Yonge's direction had its headquarters at Low Isles, and was principally engaged on experimental researches on such matters as

growth, respiration, and feeding of coral, etc. The technical results of these and other investigations of the Expedition will be published in a series of official reports. What the present book does is to give a superb popular account of the biology of corals; the formation of coral reefs; the extraordinary *congeries* of animals other than corals, and the plants, which together make up the biota of a coral reef; and finally the characteristics of the Great Barrier Reef, the longest in the world. The illustrations are numerous and extremely well done, particularly the half-tone plates, which attest the photographic skill of Mrs. Yonge, the Medical Officer of the Expedition, evidently a most versatile person.

We commend the volume unreservedly. Every school and college library should have it.



GROSSE BIOLOGEN. *Eine Geschichte der Biologie und ihrer Erforscher.*

By Ernst Almquist. J. F. Lehmanns Verlag
6.50 marks (paper) Munich

8 marks (bound) 6 x 8 $\frac{7}{8}$; 143

Professor Almquist writes on a different plan from that of many historians of science. His book is as much a critique as a presentation of the discoveries and theories of the great biologists. He feels that, under the influence of Darwinism and democracy, too little attention is paid to the constancy of species. Lamarckianism, the mutation theory, Darwinism, are all probably partial aspects of the truth.

In his account of Linné the author brings out the fact that, though in his *Fundamenta Botanica* Linné had assumed that species were originally created in their present forms, in later publications he suggested that new species might have arisen through crossing.

ANIMAL AGGREGATIONS. *A Study in General Sociology*

By W. C. Allee University of Chicago Press
\$5.00 6 x 8 $\frac{3}{4}$; ix + 431 Chicago

The social insects have long been the subject of intensive study; but so far as we are aware no one has devoted a book to what one might call sub-social life. There have been many scattered observations on the physiological results of animal aggregations, and an increasing number of workers have devoted attention to one or another phase of the problem of the influence of animals in proximity upon each other. Doctor Allee has been one of the pioneers in the systematic study of the subject, and in the present volume he has assembled a variety of phenomena from the literature and from his own experience. He particularly emphasizes the fact that there may be beneficial as well as harmful effects of crowding—a point that escaped many of the earlier observers.

The book will be disappointing to those who like neat solutions to their problems. Most of the problems remain without solution, for the present at least. But for anyone in search of problems, the book will be a joy; any chapter will offer the young researcher problems to last his next ten years.

Our only serious quarrel with the book is that the author is not rough enough. Our own reading of some of the work in this field has left us very dubious as to its real soundness, and we feel that it would have been better to have pointed out more of its shortcomings than Doctor Allee has done.



A NATURALIST IN A UNIVERSITY MUSEUM

By Alexander G. Ruthven

Alumni Press, University of Michigan
\$5.00 6 $\frac{1}{2}$ x 8 $\frac{1}{2}$; 143 Ann Arbor

A plea for the usefulness of museums in general, and university museums in particular, with statements of the policies best adapted to enable the museum to perform its functions most effectively. There are also some reflections on the kind of biology which should be taught in the secondary schools, and on the training of secondary school teachers, which seem to us sound and valuable.

GARDEN POOLS *Large and Small.*

By Leonidas W. Ramsay and Charles H. Lawrence
The Macmillan Co.
\$2.50 5 $\frac{1}{2}$ x 8 $\frac{1}{2}$; xiv + 108 New York

A useful guide for the amateur who builds his own pools. It contains all the necessary information concerning the building of garden pools, stocking them with plants and aquatic animals, care of water, mosquito control, etc. The author has made those sections dealing with types of plants to select for the pool, pool margins, and background and their cultural requirements especially helpful. The book is excellently illustrated with photographs and diagrams showing pool construction and what decorative effects to aim for. There is an index.



ESSENTIALS OF BIOLOGY

By W. H. D. Meier and Lois Meier

Ginn and Co.

\$1.68 5 x 7 $\frac{1}{2}$; vii + 529 Boston

This excellent text-book for schools emphasizes the interrelation of organisms with each other and with the physical world about them, the way in which each organism maintains its own life and the life of the species, the conservation of native plant and animal life, the development and improvement of living organisms, and their control for the health and well-being of man.

GRENZFRAGEN DES LEBENS. *Eine Umschau im Zwischengebiet der biologischen und anorganischen Naturwissenschaft*

By Friedrich Rinne

Quelle und Meyer

9 marks (paper)

Leipzig

10 marks (cloth)

$6\frac{3}{4} \times 9\frac{3}{4}$; vii + 128

A survey of the relations between the organic and the inorganic. The author concludes that there is no sharp line of division between the two realms and that some day life may be produced in the laboratory.



HUMAN BIOLOGY

THE STONE AGE CULTURES OF KENYA COLONY

By L. S. B. Leakey, with Appendices by J. D. Solomon, C. E. P. Brooks, A. T. Hopwood, H. C. Beck, and M. Connolly

The Macmillan Co.

\$9.00 $7\frac{3}{8} \times 9\frac{3}{4}$; xiii + 288 New York

This beautifully produced book opens a new chapter in archeology. While the work which it records has only just fairly begun it already gives distinct promise of leading to the establishment of a definite correlation between European and African prehistory. The basis of such a correlation is the climatic changes in the Pleistocene era. Evidence is accumulating to indicate that the glacial and interglacial periods in Europe had as counterparts in Africa pluvial and interpluvial periods, that is wetter and dryer periods. These suggested correlations are tabulated (p. 232) as follows:

Nakuran wet phase	Wet period <i>circa</i> 850 B. C.
Dry period	Climatic optimum
Makalian wet phase	Bühl stadium, etc., to climatic optimum
Dry period	Achen retreat, etc.

Gamblian pluvial. The sub-divisions are	Würm glacial
Lower Gamblian and Upper Gamblian with a mid-Gamblian pause	Riss-Würm inter-glacial
	Riss glacial
Long break with periods of faulting and volcanic activity	Mindel-Riss inter-glacial
Kamasian pluvial. Sub-divisions unknown but may include Mr. Wayland's Kafuan and Sangoan	Mindel glacial
	Günz-Mindel interglacial
	cial
	Günz glacial

The present volume gives the general archeological results of the first two seasons' excavations of the East African Archeological Expedition under the author's direction. The skeletal remains found are being worked up under the guidance of Sir Arthur Keith, and will form the subject of a later volume.

The work so far done shows beyond any possibility of doubt that many of the stone cultures of Europe have also existed in Kenya. But whether they existed at the same times in Europe and Africa has not yet been definitely settled.

Extreme care and thoroughness, coupled with commendable caution in drawing conclusions, characterize the work. The work is extensively and beautifully illustrated, chiefly with photographs and drawings of the artefacts found. There are several appendices: one on the geology of the region studied, by J. D. Solomon; the second on climatic correlations, by C. E. P. Brooks; the third on fossil mammalia found, by A. Tindell Hopwood; the fourth on mollusks, by M. Connolly; and the fifth on prehistoric man in East Africa, by Prof. J. W. Gregory, who was the first European to find a stone age tool in Kenya.

Altogether this is a contribution of first class importance to human prehistory.

THE PHYSICAL BASIS OF PERSONALITY

By Charles R. Stockard

W. W. Norton and Co., Inc.

\$3.50 $5\frac{3}{4} \times 8\frac{1}{4}$; 320 New York

In this book Professor Stockard deals, not only with the constitution of the adult, but with the hereditary and environmental factors which influence the complex process of embryonic development. The hereditary composition, which is unique for each individual, contains the potentialities of the personality, but in order to develop this personality a long series of interactions with the environment must take place.

There is no question here of the degree of importance between the genetic background and the developmental environment; neither is sufficient without the other. Without genetic basis there is no individual, and without a suitably arranged complexity of environment the complete genetic basis is unable to produce the normal individual. The interaction between the individual and the environment is continuous from the germinal beginning to the end of life, and it is mutual: each modifies and affects the other. The individual and the environment are not separate; they are parts of a larger arrangement.

In particular, changes in rate of development may have a profound influence on the finished product. If the embryonic development of an organism is retarded at a critical moment for a particular organ that organ may permanently lose its normal relation to others. Professor Stockard believes that these changes in rate of development are often caused by changes in the endocrine secretions. Thus the achondroplastic legs of dachshunds and basset hounds may be due to a hereditary disturbance of pituitary gland secretions acting only during a critical moment in the development of the embryonic limbs, while the achondroplastic skulls and vertebral columns of bull-dogs are due to a similar disturbance acting at another time. This may or may not be the secret of the

matter. Endocrine changes in the embryo are easy to postulate but difficult to check.

As to mankind Professor Stockard classifies them in two main types, the linear or long-headed, and the lateral or wide-headed, and suggests that they depend on differences in thyroid activity.

POSTURE AND PHYSICAL FITNESS
United States Department of Labor, Children's Bureau Publication No. 205

By Armin Klein and Leah C. Thomas

U. S. Government Printing Office
Washington

10 cents

 $5\frac{7}{8} \times 9\frac{1}{8}$; v + 45 (paper)

Important and interesting results have been obtained in this investigation on the effect of good body mechanics on the health and efficiency of grammar-school children. The training was given in the Williams School at Chelsea, Mass. The posture training group included 961 children. A control group of 747 received only the regular gymnastic training. The two groups were similar at the first examination in respect of age, sex, nationality, and posture grade and various physical indices. The children were mainly from the Russian Jewish district. Unfortunately space only permits a few of the findings to be mentioned. Among these are:

"At least 80 per cent of the children in each age period had poor posture. The children of the broad type of body physique had the largest percentage of good posture, and those of the thin type had the largest percentage of poor posture.

"The prevalence of poor body mechanics was strikingly reduced by posture training. During the period of observation six children in the posture class improved in posture to every one of the control children who improved."

"Good posture once acquired was maintained, on the whole, over the 2-year period of observation by the children who received two years of posture training.

"Improvement in body mechanics was associated

with improvement in health and efficiency. More of the children who started with poor posture, when given training, improved their nutrition when they improved their posture than did those who did not improve their posture."

"Improvement in body mechanics was also associated with improvement in school work. The rate of absence due to personal illness decreased in children who received posture training until it was considerably lower than that of untrained children."

"Posture training and better posture brought an improved sense of muscle position and, therefore, improved ability to direct retraction of the lower abdomen. This ability is of value in that, with practice, the retraction of the lower abdominal wall becomes habitual and steady."

"About four-fifths of the children observed had pronated feet. This condition was most frequently associated with poor body mechanics. It was more frequent among children of the thin type and was less frequent among children with good nutrition."

The records of the data collected are exhibited in graphs and tables in the paper. In an appendix is given the physical examination schedule used in the study.



CHILDREN OF WORKING MOTHERS
IN PHILADELPHIA. *Part 1. The Working Mothers. United States Department of Labor, Children's Bureau Publication No. 204*
By Clara M. Beyer

U. S. Government Printing Office
Washington

10 cents

5 $\frac{3}{4}$ x 9; iv + 39 (paper)

The report of this survey is divided into two parts. The present bulletin dealing with "The mothers" will be followed later by one on "The findings about the children of these working mothers."

The study was undertaken mainly to ascertain the relationship between the employment of mothers and the welfare of their children, but much collateral information was gleaned concerning the increasing tendency of mothers to be employed outside the home. The field survey was made in eleven districts in different parts of Philadelphia in 1928, between the months of January and Sep-

tember. For purposes of comparison information concerning non-working mothers and their children living in the same districts was gathered. Not only were the mothers interviewed but social agency, court and school records were investigated. Among some of the conclusions which are reported in this publication are the following:

The employment of mothers is affected by various factors, among the most important of which are race, nativity, nationality, and age and number of children. Of the 6,070 mothers interviewed who had one or more children under 16 years of age and had worked after marriage, 4,486 (74 per cent) were white and 1,569 (26 per cent) were negro; 51 per cent of the white mothers were foreign born. Work was less frequent among the native-born white mothers than among the foreign born and negro. However, some of the foreign-born groups—notably the Irish, Italians, and Jews—showed a marked disposition for the mother to stay at home with her children. . . . The proportion of mothers employed varied directly with the number of children and with the presence of children of pre-school age.

The report includes fifteen tables listing the data gathered. In Appendix A is given a description of the different districts surveyed and a discussion of the employment of mothers in these districts. In Appendix B are tables showing the employment of the mothers in these districts.



DJUKA. *The Bush Negroes of Dutch Guiana*

By Morton C. Kahn The Viking Press
\$3.50 5 $\frac{3}{4}$ x 8 $\frac{1}{4}$; xxiv + 233 New York

This unique group of negroes are descendants of slaves transplanted from West Africa to Guiana by the Dutch in the latter part of the seventeenth and the early part of the eighteenth centuries. The jungles of South America furnished a safe hiding place for those who managed to escape bondage. By the year 1749 so powerful had the group become that the Dutch

were obliged to make a treaty with them which gave them their independence and in addition an annual tribute. The negroes, being a proud and hardy race, have maintained their tribal government up to the present time and still receive from the Dutch officials the yearly sum of money.

The author of this book, a bacteriologist, first went to the South American tropics in 1922 to study public health measures as applied to tropical diseases. He has since made several trips for the purpose of studying the Djukas. He writes entertainingly of his experiences and observations. Anthropologists and ethnologists will find much interesting material in the book, especially in those chapters on the dance, marriage and the family, medicine and magic, Djuka talk, and West African survivals. The Djukas are very skilful in wood carving and among the many illustrations of the book are interesting examples of this art. The author includes a sketch-map, sections on phonograms and symbols, a bibliography and an index.



EDUCATION, CRIME, AND SOCIAL PROGRESS

By William C. Bagley The Macmillan Co.
\$1.20 $4\frac{3}{4} \times 7\frac{1}{4}$; xv + 150 New York

This notable book will deeply interest many parents and educators who have been distressed by the trend of education in the United States. Prof. Bagley says in his introduction:

In sharp contrast to education in most of the civilized countries, an outstanding characteristic of education in the United States is its virtually complete rejection of the disciplinary ideal in the fields both of mind and of morals. As will be shown in the following pages, the rejection of mental discipline as an ideal was not entirely—nor even chiefly—due to the teachings of educational theory. Nor is the re-

jection of the disciplinary ideal in the field of morals to be charged entirely against the theorists. In both cases, and in a quite real sense, theory has served to rationalize and justify a certain—although a somewhat inarticulate—popular demand. This condition will make it difficult to correct what is, in the writer's judgment, by far the most serious weakness of American education and the weakness with which this book will be primarily concerned.

The book contains a collection of papers, a number of which have been given as addresses before educational meetings, etc. The headings of the chapters are as follows: Two outstanding problems of American education; Some handicaps of character education in the United States; Discipline and dogma; Shibboleths and slogans in educational reform; Playing at the work of education; Through discipline to freedom; Emergent idealism; Education for adaptability.

Professor Bagley does not discard as without value many of the innovations which have crept into modern educational methods. He finds much that can be of ultimate good provided the present tendency to follow "fashions with a maximum of zeal and a minimum of discrimination" can be avoided. If this book could be used as a text for study in parent-teacher organizations and mother's clubs, as well as in more advanced educational groups for a period of several years it would have profoundly useful effects. For it is a first-rate book, full of sound sense and ripe wisdom. We recommend it to all our readers.



BIOLOGY IN HUMAN AFFAIRS.

By Walter V. Bingham, Hugh S. Cumming, Edward M. East, Morris Fishbein, Frank H. Hankins, Joseph Jastrow, Donald F. Jones, E. Kennerly Marshall, Jr., Elmer V. McCollum, Howard M. Parsbley, Arthur M. Stimson, Lewis M. Terman. Edited by Edward M. East.

Whittlesey House, McGraw-Hill Book Co.,
Inc.

\$3.50 5 $\frac{5}{8}$ x 8 $\frac{5}{8}$; xxi + 399 New York

This book discusses what biology has to offer to man in his attempt to solve the problems which his mind and his body pose for him. The chapters deal with the following topics: Biology and human problems; the prospects of the social sciences; the renaissance of psychology; educational psychology; psychology in industry; heredity; the frontiers of medicine; the outlook of public health work; physiology of to-day; zoology and human welfare; efforts to increase the food resources; diet and nutrition. In the first essay Professor East pays his respects to those who have suggested that the scientific method may not be the only way of arriving at truth.

As to there being true scientists whose tenets include belief in the possibilities of attaining knowledge through some mysterious insight which differs from all ordinary percepts and their rational consideration, I simply deny the allegation. It is a mistake to assume that when Millikan, K. T. Compton, and Pupin issue preachments in terms of theology and metaphysics, they are speaking as scientists. They are merely demonstrating how difficult it is to divest one's mind completely of the whams and whimsies learned in early childhood. These men are competent physicists who have done admirable work in their own bailiwick by using the objective methods of science. This procedure has worked well in the solution of the problems in which they have been interested. Through it they have been successful. By its means they have attained fame. Do they give honor where honor is due? Oddly enough, they do not. In their leisure hours they endeavor to show that the perplexing questions which concern man most intimately—problems of emotion, of conduct, of thought—are unassailable by these time-tried methods. They speak vaguely of man's higher nature, something above the rational, which may attain to truth by mysterious inspiration. And they are speaking of man, you understand, of that animal of the family Hominidae, whose corporeal make-up is better known than that of any other organism; whose functional activities have been the subject of experimentation for a century and a half; whose hopes, whose desires, whose emotions, whose

mental peculiarities are objective problems about which the psychologist knows almost as much as the physicist knows about the atom; and all through the application of scientific methodology. In other words, these men who have become distinguished by using scientific methods in a given field, turn to a department in which they have no accurate knowledge and maintain seriously that here the primitive folklore of the race, unsupported by the type of evidence they would demand in their own researches, is preferable to the inductive conclusions reached by scholars working objectively on the subjects involved. In doing so they merely show that a man may do excellent work in science without being a scientist at heart.



AMONG THE NUDISTS

By Frances and Mason Merrill

Alfred A. Knopf, Inc.

\$3.00 5 $\frac{1}{2}$ x 8; xviii + 247 New York

"Naked and unashamed" is the glad tidings conveyed by this pleasant piece of evangelistic writing. The authors quite evidently thoroughly enjoyed several weeks in a German nudist colony near Lübeck. Not content to let it go at that they then embarked upon a pious pilgrimage of nakedness, so to speak; imbibed the new gospel at the feet of the European masters, and then came home and wrote this book about it all. It is an entertaining treatise, at least in the descriptive portions which make up the bulk of the volume. The latter part, in which zeal to convey a Great Message and bring converts to the fold seduces its authors into trying to be philosophical and biological, did not amuse us. It is, in fact, as dull as a Christian Science tract.

Germany, it appears, is the Holy Land of nudism. Ecdysis is the order of the day, regardless of sex, age or previous condition of adiposity. In France the cult has hard sledding, and for a simple reason. The wicked and benighted Frenchmen make fun of the nudist apostles.

Doubtless no people enjoy the nude, in all its aspects, more than the French. But also no people have a keener perception of what is immediately ridiculous in an idea. And to tell them that they are unfair about it, or that health and hygiene should be considered, or to advance any earnest, soulful argument about something which they perceive to be composed of ridiculous elements, is only to make them yell with greater glee. God pity the Uplifter in France!



THE HISTORY OF THE MAYA. *From the Earliest Times to the Present Day.*

By Thomas Gann and J. Eric Thompson

Charles Scribner's Sons

\$2.50 $5\frac{1}{4} \times 7\frac{3}{4}$; x + 264 New York

A history of the Mayan civilization must, in part, be more or less an outline. Nevertheless, the authors have written a book which will be of much interest to the general reader and useful as a reference book to the student. The chapters on the Origin of the Maya, history of the old empire, art and architecture, and the modern Maya have been contributed by Doctor Gann, leader of recent expeditions of the British Museum to Central America. Doctor Thompson, assistant curator of the Chicago Field Museum, has written the sections on the history of Yucatan, religion, religious ceremonies and traditions, daily life, warfare, food and clothing, and the calendar.

The volume is well illustrated, contains a bibliography of the more important references and is well indexed.



ILLITERACY IN THE UNITED STATES

By Sanford Winston

University of North Carolina Press

\$3.00 $5\frac{1}{2} \times 8\frac{1}{2}$; xii + 168 Chapel Hill

A study, by partial correlation methods,

of the relation between illiteracy and certain social phenomena, notably birth-rate, infant mortality, age at marriage, size of family, and suicide. In general, the correlations secured are about what would be expected; they show that decreasing illiteracy is associated with decreased birth-rate and infant mortality, with increased age at marriage, with decreased size of family, and with increased suicide. Whether illiteracy is causally related to any or all of these phenomena remains, of course, an open question.



MASTER MINDS OF MODERN SCIENCE

By T. C. Bridges and H. Hessel Tiltman

Lincoln Mac Veagh, The Dial Press

\$3.00 $5\frac{5}{8} \times 8\frac{3}{8}$; 278 New York

A series of popular accounts of more or less prominent scientists and technologists. The fields of work represented are physics (8); engineering (5); agriculture, medicine, geology, chemistry, biology (2 each); astronomy and meteorology (1 each). (It might perhaps be fairer to transfer one paleontologist and one biochemist to biology.) The countries represented are England (17), the United States (2), and France, Germany, India, Italy, Poland, and Switzerland (1 each). It is perhaps fair to say that the authors expressly state that "our idea has been not merely to choose the greatest scientists of the present day, but rather to present as many different aspects of Science as possible, and to procure the material in each case from the one best able to give it."



OUTLINES OF AGRICULTURAL ECONOMICS. *Revised Edition*

By Henry C. Taylor The Macmillan Co.

\$3.25 $5\frac{1}{4} \times 7\frac{3}{4}$; xii + 614 New York

"Better farm management, better mar-

keting, better land tenure, and a better distribution of wealth which will give the farmer a fairer share of the national income as a basis of a satisfactory life, and the nation a better agriculture and a better rural population as the basis of our national life, constitute the objective in the mind of the author of this volume.

. . . . The book is intended to help toward an understanding of the principles which underlie the choice of a farm, the selection of crop and live-stock enterprises, the management of labor and equipment and the organization of these elements into an efficient going concern. Until these principles become a part of the thinking of the farmer and become a factor in guiding his actions, farming will lack efficiency. It is the action of the farmer himself that determines whether or not the farm is well managed."

A sound and useful volume, though most practical farmers of our acquaintance are too busy on the farm to read it.

AMONG THE ESKIMOS OF WALES, ALASKA 1890-93.

By Harrison R. Thornton. Edited and Annotated by Neda S. Thornton and William M. Thornton, Jr. The Johns Hopkins Press

\$4.00 $6\frac{1}{4} \times 9\frac{1}{4}$; xxxviii + 235 Baltimore

An interesting and instructive account of the Alaskan Eskimos previous to the gold discoveries. The author lived for three years at Cape Prince of Wales. He describes the natives accurately and sympathetically.

THE INBORN FACTORS IN DISEASE.

An Essay

By Archibald E. Garrod

Oxford University Press

\$2.75 (U. S. A.) London and New York

7s. 6d. net (England)

$4\frac{3}{4} \times 7\frac{1}{2}$; 160

A brief essay on the constitutional factor in disease, persuasively written by a physician of long experience. He argues for the ultimate chemical nature of individual differences:

It might be claimed that what used to be spoken of as a diathesis is nothing else but chemical individuality. But to our chemical individualities are due our chemical *merits* as well as our chemical shortcomings; and it is more nearly true to say that the factors which confer upon us our predispositions to, and immunities from the various mishaps which are spoken of as diseases, are inherent in our very chemical structure; and even in the molecular groupings which confer upon us our individualities, and which went to the making of the chromosomes from which we sprang.

An interesting book for students of human constitution.

SOURCE BOOK IN ANTHROPOLOGY.

Revised Edition.

By A. L. Kroeber and T. T. Waterman

Harcourt, Brace and Co.

\$3.00 $5\frac{1}{2} \times 8\frac{1}{2}$; viii + 571 New York

This new edition of a standard auxiliary text for courses in anthropology has been considerably altered in the revision. The selection of articles and passages for inclusion has been primarily based upon their utility in stimulating discussion. The 55 passages quoted are grouped under the following general heads: History of anthropology; evolution; heredity and race; prehistory; subsistence and material culture; social culture; aesthetic and religious culture; and dynamics of culture. The book is a valuable addition to the teachers' *armamentarium*, and is edited with sound critical judgment. There is a detailed index.

HUNGER AND LOVE

By Lionel Britton

Harper and Bros.

\$4.00 $5\frac{3}{4} \times 8\frac{5}{8}$; x + 623 New York

The story of an English shop-boy's

struggle for existence and understanding of the universe.



DAS ANTLITZ DES ALTERS. *Photographische Bildnisse von Erich Retzlaff. Einleitung von Jakob Kneip*

Pädagogischer Verlag, G. m. b. H. Düsseldorf
8.50 marks

$8\frac{1}{4} \times 11\frac{3}{4}$; 21 + 47 photographs

The viewpoint and the purpose of this beautiful volume are literary and artistic rather than scientific. The superb portraits of some 35 old men and women will, however, be of interest and use to students of human senescence, senility, and longevity. There is no index nor are the plates numbered.



THE FAMILY. *Source Materials for the Study of Family and Personality.*

By Edward B. Reuter and Jessie R. Runner
McGraw-Hill Book Co., Inc.

\$4.00 $5\frac{3}{4} \times 9$; x + 615 New York

A source book which treats the adaptation of the family form to conditions in other times and places, the development of personality within the family group, and the adjustment of the family and its members to modern environment.



ANTHROPOLOGISCHE UNTERSUCHUNGEN IN ZÜRCHER KINDERGÄRTEN MIT BERÜCKSICHTIGUNG DER SOZIALEN SCHICHTUNG. *Inaugural-Dissertation zur Erlangung der philosophischen Doktorwürde vorgelegt der Philosophischen Fakultät II der Universität Zürich.*

By Bertha Niggli-Hürlimann

Art. Institut Orell Füssli

$6\frac{3}{4} \times 9\frac{3}{4}$; 215 (paper) Zurich

The author bases her work on the measurements of 702 children aged 4 to 7

years. The children of the well-to-do classes are taller and heavier than those of the poor, and have broader shoulders, but do not differ from them in breadth of hips or chest circumference.



THE PROMOTION OF THE WELFARE AND HYGIENE OF MATERNITY AND INFANCY. *The Administration of the Act of Congress of November 23, 1921. Fiscal Year Ended June 30, 1929. United States Department of Labor, Children's Bureau Publication No. 203*

U. S. Government Printing Office
25 cents Washington

$6 \times 9\frac{1}{8}$; vi + 142 (paper)

This report is arranged under the following headings: Summary of state activities during 1929; Seven years' work of the cooperating states under the maternity and infancy act; Principal activities of individual states, 1929; Federal administration during 1929; and The services of the Children's Bureau under the maternity and infancy act. In a group of four appendices is given information on (a) the text of the act for the promotion of the welfare and hygiene of maternity and infancy and of supplementary legislation; (b) administrative agencies and officers; (c) infant and mortality rates; and (d) publications and exhibits of the Children's Bureau bearing upon maternal, infant, and child welfare and hygiene.



ZOOLOGY

A HISTORY OF ENTOMOLOGY

By E. O. Essig *The Macmillan Co.*

\$10.00 $5\frac{1}{2} \times 8\frac{1}{2}$; vii + 1029 New York

A valuable contribution to the history of entomology. The author, professor of entomology at the University of Cali-

for California and entomologist at the California Agricultural Experiment Station, has maintained essentially a western viewpoint throughout the treatise. With the rapid development of the West, particularly in agriculture and commerce, there has been an enormous development in entomological problems. These problems have received the attention of numerous investigators from the United States Division of Entomology, colleges and experiment stations. In order to trace the progress of these investigations and to preserve historical material which has been in danger of becoming more obscure as time goes on the author has written this book. The first eight chapters deal with the following subjects; Prehistoric entomology; California Indians in relation to entomology; historical background; principal institutions in California featuring entomology; some historical facts concerning the more important orchard mites and insects of California; the biological control of insect pests; insecticides; entomological legislation. Chapter IX includes nearly 300 pages and is devoted to biographical sketches. The author was unable because of lack of space to include many of those who have contributed to the development of entomology in California. His selection was as follows:

(1) some of the great founders of entomology whose influences are world-wide; (2) the fathers of entomology in North America, who established the science in this country and who described many western insects; and (3) the pioneer collectors, investigators, and teachers, who at some time worked within the confines of the state or described material taken here. In numerous instances these sketches are accompanied by photographs of individuals. Chapter X gives a chronological table showing the development and progress of entomology in relation to history and other sciences.

The work contains many figures and a number of tables. It is well documented and indexed.

A TEXTBOOK OF AGRICULTURAL ENTOMOLOGY

By *Kenneth M. Smith* The Macmillan Co.
\$4.25 $5\frac{1}{2} \times 8\frac{1}{2}$; xiii + 285 New York

This book has been written for the advanced student, the agriculturist and the agricultural entomologist of the British Isles. While there is necessarily something of compilation in the book the author includes much original work. The elements of entomology have been omitted, since these are already adequately treated in a number of modern books. Insect pests of fruit have also been excluded, partly because of lack of space and partly because of the existence of a comprehensive book on them. The author, on the whole, has admirably succeeded in his aim to produce an up-to-date comprehensive treatise without being profuse. He has dealt with each insect in considerable detail, giving descriptions of the adult and its various stages and the main points in its life history. Control methods are given special attention. In each case the more important farm weeds which act as alternate hosts for many insects are given and also the natural enemies so far as these are known. The book is adequately illustrated and each chapter is well documented. There is an appendix on characteristic symptoms of insect attack, and on common farm weeds in relation to insect pests. In addition to the general index there are indices of authors and of parasites and predators.



THE BLOOD OF NORTH AMERICAN
FRESH-WATER MUSSELS UNDER
NORMAL AND ADVERSE CONDI-
TIONS. *U. S. Department of Commerce,
Bureau of Fisheries Document No. 1097.*
By *M. M. Ellis, Amanda D. Merrick, and
Marion D. Ellis*

U. S. Government Printing Office
20 cents $7\frac{1}{2} \times 11$; 34 (paper) Washington

Within recent years mussel beds of the upper Mississippi, which formerly were productive of shells on a commercial basis, have contained large numbers of dead and dying animals. This condition seems to have been produced by a change in the natural habitat of the mussel due to water contamination by municipal and industrial wastes, and navigation. In the fresh water mussels there is a very large volume of blood which, aside from its ordinary functions, is important in the locomotion of the animals. During activity, the foot expands to many times its retracted volume by an inflow of blood which can be retained there. When the foot is drawn within the shell the blood flows into numerous sinuses or reservoirs in various parts of the body.

This study of the physiological condition of the blood of twenty-seven species of North American fresh-water mussels shows it to be very low in solids as compared with the blood of other animals, both fresh water and marine. It is more alkaline than that of most animals. Although the blood contains only very small quantities of inorganic salts, these salts are balanced against each other as in higher animals. If the proportions or the quantities of these salts in the blood change within rather narrow limits, the activity of the heart and of the foot of the mussel ceases promptly. Mussels are very sensitive to changes in the salt content of the water in which they live. Because of their limited locomotion, changes in the water composition of their habitat produce within a few hours changes in the specific gravity and salt content of the blood.

Tables and charts in the paper exhibit the results of the various blood analyses. There is a bibliography.

NATURAL HISTORY OF THE BAY SCALLOP. *U. S. Department of Commerce, Bureau of Fisheries Document No. 1100.*

By James S. Gutsell

U. S. Government Printing Office
30 cents 7½ x 11; 64 (paper) *Washington*

The bay scallop (*Pecten irradians*) is of considerable economic value, ranking third among American molluscs. Along the Atlantic Coast it ranges from Massachusetts to the Gulf of Mexico. Up to the present little has been known concerning its life history or its relation to its environment. This paper represents a comprehensive study of the natural history of the scallop. Particularly has the author studied in detail those phases which seemed to be of greatest importance in conservation. The work includes anatomical drawings and figures of developing embryos, growth curves, and charts showing the effect of varying salinity and temperature of the sea water upon mortality. There is a lengthy bibliography.



BIRD BANDING BY SYSTEMATIC TRAPPING. *Scientific Publications of the Cleveland Museum of Natural History, Vol. I, No. 5*

By S. Prentiss Baldwin

Cleveland Museum of Natural History
75 cents 6¼ x 9¼; 44 (paper) *Cleveland*

In this publication are reprints of two of the author's papers previously published elsewhere: *Bird banding by means of systematic trapping*, and *The marriage relations of the house wren*. The bird banding method discussed in the first paper was adopted by the U. S. Biological Survey in 1920 and the paper was issued as an instruction book on the subject. The author describes the methods of baiting and trapping in full, also a home record system

which is simple but effective. He includes examples of his findings. While it was possible for Mr. Baldwin to give only a limited amount of time to the work yet his results were surprising. How useful this method has been to the U. S. Biological Survey will be seen in the report which is made for the year 1930. During the year 1750 bird banders placed 182,263 bands and had return records on 10,000 banded birds.

In the second paper in this publication there is reported the results of records made on the mating of wrens and on incubation periods. The author has records on three generations of wrens in direct line, and numerous uncles, aunts, cousins, brothers and sisters. Apparently there is no inseparable bond between the mated birds. They have even been found to choose new mates for a second brood during the same season.

Both papers contain tabulations and record data. There are a number of illustrations.

ECOLOGICAL STUDIES OF THE BEET LEAF HOPPER. *United States Department of Agriculture Technical Bulletin No. 206*
By Walter Carter

U. S. Government Printing Office
30 cents $5\frac{3}{4} \times 9$; 115 (paper) Washington

A comprehensive study of *Eutettix tenellus* Baker, both in its native desert environment and in the beet field. It consists of an investigation of the

relationships of the insect to its host plants and the relationships of the insect and the host plants to the desert, with its extreme physical factors of moisture and temperature. The possible explanation for the migration of the insect from the desert to the beet fields involves a study of all the factors of both environments which make for large *Eutettix* populations and their successful establishment in the beet fields. The fact that the insect transmits a virus which causes a disease of the beets necessitates the

consideration of this disease, the insect's transmission of it, and the beet's susceptibility to it

Incorporated in the paper are numerous tables and diagrams exhibiting data collected on all the points studied. There is a bibliography of 32 titles.

BIRDS OF ARKANSAS. *University of Arkansas, College of Agriculture, Agricultural Experiment Station Bulletin No. 258.*

By W. J. Baerg

Agricultural Experiment Station
Fayetteville, Ark.
76 cents

6 x 9; 197 (paper)

The chief value of this bulletin would seem to be in the information which it gives to the agriculturist concerning the economic value of birds, although teachers of nature study classes and bird lovers will find it a useful guide in field work in the Arkansas region. Three hundred and twelve species and sub-species are listed and described. Notes on the feeding and nesting habits, song and call notes, migration and other phases of bird life accompany the descriptions. No colored plates are included in the work and only 37 black and white illustrations. There are tables showing migration records, song period, and average song periods. The index contains both common and scientific names.

A MANUAL FOR THE STUDY OF INSECTS. *Revised Edition.*

By John H. Comstock, Anna B. Comstock and Glenn W. Herrick

The Comstock Publishing Co.
\$4.00 $6\frac{1}{4} \times 9\frac{1}{4}$; xiii + 401 Ithaca, N. Y.

At Professor Comstock's request Prof. Glenn W. Herrick took over the task of revising this book, which has already passed through eighteen editions since it first appeared in 1895. The aim of the author to make it more elementary has

been carried out by Professor Herrick. At the same time, in form and arrangement there has been little change. The subject matter has been brought up to date, but in order to meet the requirements of beginning courses in entomology the book has been simplified and condensed. While some of the old figures have been omitted, many new ones have been added.

This volume should be on the bookshelves of all biology laboratories. For teaching purposes it is invaluable. Even the layman who has some curiosity about insects will not find it too formidable. Once within its pages he will find much that is interesting and stimulating.



NATIONAL INSTITUTE OF HEALTH
BULLETIN NO. 155. 1. *Key Catalogue of Parasites Reported for Chiroptera (Bats) with Their Possible Public Health Importance*, by C. W. Stiles and Mabelle O. Nolan. 2. *The Confused Nomenclature of Nycteribia Latreille, 1796, and Spinturnix Heyden, 1826*, by Benjamin J. Collins.

U. S. Government Printing Office
30 cents Washington

5 $\frac{3}{4}$ x 9 $\frac{1}{8}$; iv + 186 (paper)

Much careful work has gone into the preparation of these two papers, which will interest taxonomists chiefly. The public health importance of bats is not likely to be apparent at first thought, but it is discussed under six headings as follows: A. Bats as food; B. Bats as blood-suckers; C. Bats as distributors of bed-bugs; D. Bats as household pets; E. Bats as destroyers of mosquitoes; F. Bats as reservoirs of disease.



RELATIVE GROWTH AND MORTALITY OF THE PACIFIC RAZOR CLAM (*SILIQUA PATULA*, DIXON) AND THEIR BEARING ON THE COMMER-

CIAL FISHERY. U. S. Department of Commerce, Bureau of Fisheries Document No. 1099.

By F. W. Weymouth and H. C. McMillin

U. S. Government Printing Office
15 cents 7 $\frac{1}{2}$ x 11; 24 (paper) Washington

This paper is one of a series of studies on molluscs of the Pacific Coast of North America. It deals with the relationships

of the most abundant and only commercially important species, *Siliqua patula*. The variability, mortality, and sexual differences within the species are discussed. Data on the growth of clams from 10 localities are presented, together with a discussion of methods employed and localities considered. Similarities shown by the growth data and the conception of growth to which they lead is given, and a critical examination of the graphic representation and terminology follows. The differences exhibited by the various localities are discussed.

The authors include in their report tables of measurements and growth curves. There is a bibliography of 35 titles.



PADDLEWINGS. *The Penguin of Galápagos*.

By Wilfrid S. Bronson

The Macmillan Co.
\$2.00 7 $\frac{1}{2}$ x 8 $\frac{1}{4}$; 106 New York

An amusing book for young folks, particularly those to whom the New York Aquarium is accessible, wherein dwells the hero of this whimsical story. The author has spent many years at sea drawing and painting marine animals, and incidentally studying animal behavior. A good deal of natural history of the animals to be found in the region of the Galápagos Islands serves as the background for the thrilling experiences of this young penguin. The drawings will delight all intelligent children.



DEVELOPMENT AND LIFE HISTORY OF FOURTEEN TELEOSTEAN FISHES

AT BEAUFORT, N. C. U. S. Department of Commerce, Bureau of Fisheries Document No. 1093.

By Samuel F. Hildebrand and Louella E. Cable. U. S. Government Printing Office

35 cents $7\frac{1}{2} \times 11$; 106 (paper) Washington

The teleosts which this paper deals with are as follows: *Anchoviella epsetus* (Bonnaterre) and *Anchoviella mitchilli* (Cuvier and Valenciennes), anchovies. *Orthopristis chrysopterus* (Linnaeus), pigfish, hogfish. *Bairdiella chrysura* (Lacépède), white perch, sand perch. *Leiostomus xanthurus*, (Lacépède), spot. *Micropogon undulatus* (Linnaeus), croaker, hardhead. *Parexocetus mesogaster* (Bloch), short-winged flyingfish. *Cypselurus furcatus* (Mitchell), four-winged flyingfish. *Decapterus punctatus* (Agassiz), scad, cigarfish, round robin. *Seriola dumerili* (Risso), amberfish, rudderfish. *Paralichthys dentatus* (Linnaeus) and *Paralichthys albiguttus* (Jordan and Gilbert), summer flounder, southern flounder. *Symphurus plagiusa* (Linnaeus), tongue-fish, sole. *Monacanthus hispidus* (Linnaeus), foolfish.

Numerous drawings illustrate the development of the various forms, and tables and curves show the rate of growth. There is a bibliography of fifteen titles.

PAPERS FROM TORTUGAS LABORATORY OF CARNEGIE INSTITUTION OF WASHINGTON. Vol. XXVII. Carnegie Institution of Washington Publication No. 413

Carnegie Institution of Washington
\$7.00 (cloth) Washington
\$6.00 (paper)

$9 \times 11\frac{5}{8}$; 105 (paper)

This volume contains papers on A cytological and biochemical study of the ovaries of the sea-urchin *Echinometra lucunter*, by D. H. Tennent, M. S. Gardiner and D. E. Smith, in which the authors conclude

that Golgi bodies and chondriosomes are not structural elements in the cellular architecture but the chemical products of physiological processes; *Observations on the formation of the egg of Echinometra lucunter*, by Ruth A. Miller and Helen B. Smith; *Studies on the coral reefs of Tutuila, American Samoa, with especial reference to the Alcyonaria*, by Lewis R. Cary; and *Formed components and fertilization in the egg of the sea-urchin Lytechinus variegatus*, by Esther C. Hendee.

COLLEGE ZOOLOGY. Third Edition.

By Robert W. Hegner The Macmillan Co.
\$3.50 $5\frac{1}{2} \times 8\frac{1}{2}$; xxiii + 713 New York

In the revision of this standard textbook a chapter on Heredity and Genetics has been added but the general plan of the book, with its emphasis on function as well as on structure, has not been altered.

LABORATORY GUIDE FOR COLLEGE ZOOLOGY

By Robert W. Hegner The Macmillan Co.
\$1.00 $5\frac{1}{2} \times 8\frac{1}{2}$; viii + 75 New York
This laboratory guide is designed for use with the author's *College Zoology*.

TRICHOMONAD FLAGELLATES FROM TERMITES. II. *Eutrichomastix*, and the Subfamily Trichomonadinae. University of California Publications in Zoology Vol. 36, No. 10.

By Harold Kirby, Jr.

University of California Press
\$1.25 $7 \times 10\frac{3}{4}$; 92 (paper) Berkeley

SPECIES OF COCCIDIA IN CHICKENS AND QUAIL IN CALIFORNIA. University of California Publications in Zoology, Vol. 36, No. 9.

By Dora P. Henry

University of California Press
25 cents $7 \times 10\frac{3}{4}$; 14 (paper) Berkeley

CRITICAL COMMENTS ON MAMMALS FROM UTAH, WITH DESCRIPTIONS OF NEW FORMS FROM UTAH, NEVADA AND WASHINGTON. *University of California Publications in Zoology Vol. 37, No. 1.*

By E. Raymond Hall

University of California Press
25 cents 7 x 10½; 13 (paper) *Berkeley*



THE MORPHOLOGY OF EUPOTERION PERNIX GEN. NOV., SP. NOV. *A Holotrichous Ciliate from the Intestine of Acmaea Persona Eschscholtz. University of California Publications in Zoology, Volume 36, No. 8.*

By Ronald F. MacLennan and Frank H. Connell

University of California Press
25 cents 7 x 10½; 16 *Berkeley*



BOTANY

TAXONOMY OF THE FLOWERING PLANTS

By Arthur M. Johnson *The Century Co.*
\$7.50 5¼ x 6½; xxi + 864 *New York*

This book is outstanding for its clearness and simplicity. The author, associate professor of botany in the University of California at Los Angeles, has had many years of teaching taxonomy. While intended for class-room use this volume will also be found useful by gardeners, horticulturists, foresters and nature lovers, and as a reference book for school and public libraries. The pen and ink drawings are a valuable feature of the book. These are numerous, well selected, and are executed with much skill. Quite aside from their illustrative value is the training which they give the student in acquiring a knowledge of what fundamental structures are of value in classification. Especial emphasis is placed by the author on the

importance of diagrammatic and semi-diagrammatic drawings in making the study of taxonomy simple and effective.

The book is in two parts. The first nine chapters deal with the fundamental principles of flower analysis. The second part, also containing nine chapters, deals with systematics. There is a detailed and well arranged glossary. The bibliography contains many titles, also special sections on geological and paleontological references, ecology, history of botany, periodicals etc. There is an index for topics and one for figures. In spite of its 864 pages the book is not unduly heavy.



MAIZE IN SOUTH AFRICA

By A. R. Saunders

Central News Agency, Ltd.
20 shillings net *Johannesburg, South Africa*
5½ x 8½; 284

The total production of maize in South Africa is in general comparatively small. This is due in large part to geographic and climatic features and soil conditions. Nevertheless the author of this book shows how much can be done to offset these adverse conditions by proper selection of locality and seed, soil preparation, and after culture. Agriculturists in South Africa will find this treatise invaluable, while readers of general biological literature will find much in it that is interesting. The author is Senior Research Officer (Summer Cereals) of the Department of Agriculture of the Union of South Africa. After an introductory chapter on the history, origin, and importance of maize, he takes up in detail various phases of maize culture. There are chapters on statistics of production, climate in relation to maize production, soils, fertilizer practice and crop rotation, planting, cultivation, and harvesting. Considerable space is given to the botany of maize, the varieties, and

inheritance, breeding, and seed selection. There are also sections on diseases of maize and insect pests, the uses of maize, and maize in commerce.

The work concludes with a lengthy bibliography and an index.



PLANT PHYSIOLOGY. *With Reference to the Green Plant.*

By Edwin C. Miller

McGraw-Hill Book Company, Inc.

\$7.00 $5\frac{3}{4} \times 9$; xxiv + 900 New York

The author of this excellent textbook has had as a background for his work twenty years of teaching in the Kansas State Agricultural College, and the same number of years as plant physiologist in the Kansas Agricultural Experiment Station. His book has been designed for upper class men and graduate students. It will also be of value as a reference book in biological laboratories, both for students and investigators. Treating only of the physiology of green plants the author has incorporated into his book summaries of all the important researches of plant physiologists. The entire field is well and adequately covered. The arrangement of the material is excellent. An important feature of the book is the lengthy series of questions at the end of each chapter. To each chapter is also appended detailed reference lists. There are author and subject indices.



LIFE MOVEMENTS IN PLANTS. *Transactions of the Bose Research Institute, Calcutta, Vol. VI, 1930-1931.*

Edited by Sir Jagadis Chunder Bose

Longmans, Green and Co.

18s/net

\$7.20

London and New York

$5\frac{1}{2} \times 8\frac{3}{4}$; vi + 211

We have not found anything of momen-

tous consequence in the present volume which will not be familiar to readers of Bose's previous works. The experiments described are interesting; but there is almost complete failure to notice the work and opinions of other investigators.



HANDBUCH DER BIOLOGISCHEN ARBEITSMETHODEN. *Lieferung 353. Containing following articles: Methodik der Herstellung pflanzlicher Aschenbilder und Kieselenskelette sowie von Antbrakogrammen, and Die Anfertigung von Dünnschliffen von rezenten pflanzlichen Materialien, by Josef Kisser; Die Schliffmethoden in der Paläobotanik, by Karl A. Jurasky; Die Mazerationismethoden für rezente Pflanzengewebe, by Josef Kisser; Die Mazerationismethoden in der Paläobotanik, by Karl A. Jurasky; Die kryoskopische Bestimmung des osmotischen Wertes bei Pflanzen, by Heinrich Walter.*

Urban und Schwarzenberg

10 marks 7×10 ; 179 (paper) Berlin

This number of the *Abderhalden Handbuch* is largely devoted to methods for the microscopic examination of plant tissues.



KEIMUNGSPHYSIOLOGIE DER GRÄSER (GRAMINEEN). *Eine Lebensgeschichte des reifenden, ruhenden und keimenden Grassamens.*

By Ernst Lehmann and Fritz Aichele

Ferdinand Enke

60 marks (paper)

Stuttgart

63 marks (cloth) $6\frac{1}{2} \times 10$; xxiii + 678

The questions involved in the development and sprouting of seeds are of great theoretical and practical importance. In this voluminous work the authors synthesize the present knowledge of this field for the cereals. There is a bibliography of 75 pages and an index.

SOME FAMILIAR WILD FLOWERS

By James E. Jones The Macmillan Co.
\$1.50 $4\frac{3}{4} \times 7\frac{1}{4}$; 90 New York

A pocket guide containing excellent photographs with brief descriptions.



MORPHOLOGY

CONCERNING, *Earliest First Growth in the Human Ovum; Origin of First Blood Corpuscle and Plasm—First Blood Space and Vessel—The Three Blood Circulations—Blood Corpuscle Differentiation from First Multinucleolated Uncolored Nucleus-Blood-Corpuscle to the Final Non-Nucleated Red Blood Corpuscle of Maturity—the Erythrocyte—the Red Blood Plastid of Minot—Origin of the Cancer.*
By Frank A. Stahl Frank A. Stahl

6 x $9\frac{1}{4}$; 157 Hamilton Club, Chicago

The gist of Dr. Stahl's doctrine is as follows:

"This search for the First Blood Corpuscle; its rapid differential proliferation; division, multiplication, etc., naturally stirred up relative queries.

"In the one case the primal syncytial nucleus-cellule gives rise to the first blood corpuscle. Its polynucleoli render fierce and rapid multiplication and differentiation, to the and forming the blood corpuscles of the first or primal blood circulation.

"In another direction this syncytial proliferation develops the pseudodecidua in the placentation of the extrauterine pregnancy; as is well known this function is autogenous in the uterine pregnancy.

"Here are two differing expressions and unequal in spread and substance, yet carefully limited in both spread and substance, in these two distinct and separate loci of placentation and pregnancy. How explain this unequal development in position, spread and substance?

"Both are under a normal growth control ion or hormone principle. And as is well known, there where this control lags or is decreased there the benign placental polyp; this at times going on to malignant expression. Why, because of loss or lack of this normal growth control ion over proliferation."

ANATOMIE UND PATHOLOGIE DER SPONTANERKRANKUNGEN DER KLEINEN LABORATORIUMSTIERE. Kaninchen. Meerschweinchen. Ratte. Maus. By H. J. Arndt, C. Benda, J. Berberich, J. Fiebiger, E. Flaum, E. Haam, F. Heim, A. Hemmert-Halswick, E. Hieronymi, R. Jaffé, W. Kolmer, A. Lauche, E. Lauda, W. Lenkeit, K. Löwenthal, R. Nussbaum, B. Ostertag, E. Petri, E. Preissecker, L. Rabinowitsch-Kempner, P. Radt, Ph. Rezek, W. Robrschneider, H. Schlossberger, Ph. Schwartz, O. Seifried, R. Weber, W. Worms. Edited by Rudolf Jaffé.

Julius Springer

98 marks (paper)

Berlin

$6\frac{1}{2} \times 9\frac{5}{8}$; xix + 832

102 marks (bound)

This book on the normal and pathological anatomy of rabbits, guinea pigs, rats, and mice, is intended to help the experimenter in deciding whether the results which he observes were caused by his experimental procedure or by a spontaneous illness of the animal. It is an extremely valuable addition to the working reference literature of biology and experimental medicine.



ERKENNTNIS zugleich *Annalen der Philosophie* Band IX, Heft 5, im Auftrage der Gesellschaft für empirische Philosophie Berlin und des Vereins Ernst Mach in Wien. Band I, Heft 5.

Edited by Rudolf Carnap and Hans Reichenbach

Felix Meiner

4 marks $6\frac{1}{4} \times 9\frac{1}{4}$; 80 (paper) Leipzig

The present number of this philosophical journal contains articles by Friedrich Kraus on *The Problem of Unity and Multiplicity from the Biological Standpoint*, and by Ludwig von Bertalanffy on *Facts and Theories of Morphogenesis as an Approach to the*

Problem of Life. The latter is of first rate importance.



VEINS IN THE ROOF OF THE BUCCOPHARYNGEAL CAVITY OF SQUALUS SUCKLII. *University of California Publications in Zoology, Vol. 37, No. 3.*

By J. Frank Daniel and L. H. Bennett

University of California Press
Berkeley

25 cents

7 x 10 $\frac{3}{4}$; 6 (paper)



FEATURES IN THE DEVELOPMENT OF AMMOCOETES. *University of California Publications in Zoology, Vol. 37, No. 4*
By J. Frank Daniel

University of California Press
25 cents 7 x 10 $\frac{3}{4}$; 12 (paper) Berkeley



PHYSIOLOGY AND PATHOLOGY

ADVENTURES IN BIOPHYSICS

By A. V. Hill

University of Pennsylvania Press
\$3.00 6 x 9; ix + 162 Philadelphia

There are few scientists who can write more interestingly of difficult subjects than A. V. Hill. The present volume is no exception. It consists of five lectures given before the Johnson Foundation for Medical Physics. The subjects are: Some adventures with vapour pressure; the state of water in tissues; the conception of the steady state; the time-relations of events in muscular contraction; the mechanics of muscular contraction and other matters.



LE DOSAGE DES SELS BILIAIRES DANS LA BILE ET LE LIQUIDE DUODÉNAL

By Louis Cuny

Masson et Cie
30 francs 6 $\frac{3}{8}$ x 9 $\frac{3}{4}$; 222 (paper) Paris

This appears to be an excellent study of the problem of measuring quantitatively the excretion of bile salts. The literature from every land has been well gone over and the authors have made a number of contributions besides. There is a fine bibliography.

The book should be in the hands of everyone who is interested in this difficult problem.



THE PATHOLOGY OF INTERNAL DISEASES

By William Boyd

Lea and Febiger
\$10.00 net 5 $\frac{3}{4}$ x 9 $\frac{1}{4}$; 888 Philadelphia

This book not only treats the pathological anatomy, and in many cases the pathological physiology, of internal diseases but correlates them with clinical symptoms. It is excellently illustrated and contains bibliographies and an index.



LA PRESSION VEINEUSE PÉRIPHÉRIQUE. *Étude Physiologique, Clinique et Thérapeutique*

By Maurice Villaret, Fr. Saint Girons and L. Justin-Besançon.

Masson et Cie
38 francs 6 $\frac{1}{4}$ x 9 $\frac{1}{4}$; 318 (paper) Paris

We have here a satisfactory and useful review of what work has been done so far on venous pressure in health and disease. Unfortunately the study of this subject does not, as yet, seem to have been of much help to the physician who is attempting to diagnose and treat diseases of the circulatory system.

There is a good bibliography, in which workers foreign to France are well represented. The index is satisfactory. The work should be in the library of everyone who is interested in this subject.



LE GLYCOGÈNE dans le Développement des Tumeurs des Tissus Normaux et des Êtres Or-

ganists. Physiologie Normale et Pathologique.

By A. Brault *Masson et Cie*
80 francs 6½ x 10; 367 (paper) Paris

The researches which are recorded in this book led Dr. Brault from the occurrence of glycogen in cancers to its rôle in the normal development of different organisms, including the invertebrates and protozoa. He concludes that "glycogenesis is a universal function inherent in the very constitution of the protoplasm and completely independent from one organ to another."



LEHRBUCH DER ALLGEMEINEN PHYSIOLOGIE.

With the collaboration of L. Asher, W. von Buddenbrock, E. Gellhorn, C. Oppenheimer, J. Spek. Edited by Ernst Gellhorn

Georg Thieme
Leipzig

47 marks (paper)
49.50 marks (cloth)

6¾ x 10; xiii + 741

This book deals with the physical and chemical processes which condition vital phenomena. The topics treated are as follows: the cell as a physico-chemical system; chemistry of the cell processes; energetics of living substance; the cell as a morphological system; general physiology of development and morphogenesis; general physiology of stimulation; tropisms. There are bibliographies for each section, and an index.



BIOCHEMISTRY

**KOSTYCHEV'S CHEMICAL PLANT
PHYSIOLOGY.** *Authorized Edition in
English with Editorial Notes.*

By S. Kostychev (Translated and edited by
Charles J. Lyon) P. Blakiston's Son and Co.,
Inc.

\$6.00 net 6 x 9½; xv + 497 Philadelphia

A translation, revised and brought down to date by the author, of a volume which appeared in German in 1926. There are chapters on: The foundations of chemical plant physiology; the assimilation of solar energy by green plants and the primary synthesis of organic compounds; chemosynthesis and the assimilation of molecular nitrogen; plant nutrition with prepared organic compounds; the mineral nutrition of plants; carbohydrates and proteins; the transformations of these substances in the plant; secondary plant substances; respiration and fermentation.

The book will be a useful one to English speaking students.



SEX

IDEAL MARRIAGE. *Its Physiology and
Technique*

By Th. H. Van de Velde. Translated by
Stella Browne. *Covici, Friede, Inc.*

\$7.50 New York

5¾ x 8½; xxvi + 323 + 7 plates

This book is a detailed manual of the technique of the art and mystery of human copulation. When we say this we mean it. Nothing is left either out or to the imagination. It is precise, detailed, and scientifically accurate on every *minutia* of the business to which it addresses itself. It is a pedantically humorless treatise about a subject, which many wiser men than its author long ago perceived to be essentially as ridiculous as it is pleasant and biologically necessary.

Naturally such a book is well suited to a civilization so little subtle as ours today is. It has had a great sale in its original German dress. There is every reason to suppose that this English translation will be equally successful. Reginald the Office Boy has already sent off three copies as wedding presents; but, with that sagacity

far beyond his years which he occasionally displays, says he believes that the greatest sphere of usefulness of this book will be in our coeducational institutions.

Theoretically the sale of the book is "positively restricted to physicians, lawyers, ministers, educators and social workers." Anyone, if there should be anyone, not coming within these categories when constructively interpreted, may take comfort in the thought that the 18th amendment to the constitution theoretically restricts the sale of alcoholic beverages.



BIOMETRY

CORRELATION ALINEMENT CHARTS IN FOREST RESEARCH. *A Method of Solving Problems in Curvilinear Multiple Correlation.* U. S. Department of Agriculture Technical Bulletin No. 210.

By Donald Bruce and L. H. Reineke

U. S. Government Printing Office
15 cents 5 $\frac{3}{4}$ x 9; 88 (paper) Washington

A development of the theory of correlation, partially graphic in its technique, which has a wide applicability to forestry problems, many of which have hitherto seemed insoluble. So technical a subject cannot be adequately discussed briefly, but its importance can be indicated by listing some of the problems to which it can be applied successfully. Among these are: decomposing dextrose by sulphuric acid at high temperatures; bark thickness; damping-off of coniferous seedlings in which the variables have a periodic character; cell-sap density or osmotic pressure with site quality; soil and air temperatures; soil moisture; relation of resin flow to size and age of tree and to climatic factors; viability of seed, as affected by size, weight, age and storage temperatures. In nursery practice, size of plants may be related to amount of fertilizer or other chemicals, amount of water and

growing space. Skidding time, or cost, in logging studies may be correlated with log diameter, length, and skidding distance, or sawing time in the mill may be correlated with size, amount of defect, etc. In pulp and paper investigations, yields or breaking strength may be related to composition of liquor, temperature, pressure, duration of cook, percentages of species or types of pulp, etc.

Included in the paper are numerous tables and figures exhibiting regression lines, curves, alinement charts, etc. In an appendix will be found short cut methods in handling the statistical material. There is a bibliography of 48 titles.



AN INTRODUCTION TO MEDICAL STATISTICS

By Hilda M. Woods and William T. Russell

P. S. King and Son, Ltd.

7s. 6d. net 4 $\frac{3}{4}$ x 7 $\frac{1}{8}$; x + 125 London

This little book was prepared as a text for students taking the course for the Diploma in Public Health in the London School of Hygiene and Tropical Medicine. In little more than a hundred pages it gives a considerable amount of information on the sources of vital statistics—the census and registration of births, deaths, and sickness—on tabulation of data, graphs, population estimates, birth and death rates, standardized rates, averages, measures of dispersion, correlation and regression, life tables, and sampling. Though the student who masters it will not yet be an expert statistician, he will have had a sound introduction to medical statistics, and the authors hope that this will whet his appetite for more.



STATISTICAL TABLES AND GRAPHS

By Bruce D. Mudgett

Houghton Mifflin Co.

\$1.75 5 x 7 $\frac{1}{2}$; viii + 194 Boston

This book is designed "not for the students who intend later to become statisticians, but rather for those who intend to become business men, and emphasis has been placed on those elementary statistical methods with which business men are likely to come into most intimate contact." The matter is sound and well presented. In spite of the author's disclaimer we feel that statisticians, as well as business men, will profit by reading the book.



AN ELEMENTARY TREATISE ON ACTUARIAL MATHEMATICS

By Harry Freeman *The Macmillan Co.*
\$8.50 $5\frac{1}{2} \times 8\frac{1}{2}$; xiii + 399 New York

A well-written textbook, which should be of some value to others than prospective actuaries. The subjects treated, and the space allotted, are as follows: trigonometry, 21 pages; finite differences and interpolation, 112 pages; functions and limits, 17 pages; differential calculus, 73 pages; integral calculus, 91 pages; and probability, 57 pages. There is an extended collection of problems.



THE SMOOTHING OF TIME SERIES

By Frederick R. Macauley
National Bureau of Economic Research, Inc.
\$2.00 6×9 ; 172 New York

A study of various methods of smoothing, with extensive illustrations, which will be useful to anyone who has to deal with time series. We should have liked, however, to have had included a discussion of the broader aspects of the problem; in particular, as to when smoothing is justified, as to how much labor is warranted, and as to the meaning to be attached to differences in results obtained by different methods of smoothing.

SOME RECENT RESEARCHES IN THE THEORY OF STATISTICS AND ACTUARIAL SCIENCE

By J. F. Steffensen *The Macmillan Co.*
\$2.00 $5\frac{1}{2} \times 8\frac{1}{2}$; vii + 48 New York

Three lectures on various points of statistical and actuarial theory. Of particular interest are the discussion of presumptive values of frequency constants and of the theoretical foundations of the Pearsonian and the Gram-Charlier frequency curves. The author objects to presumptive values, on the ground that their use leads to theoretical contradictions; and he expresses the opinion that the Pearsonian curves are of more general utility than the various series expansions.



PSYCHOLOGY AND BEHAVIOR

BRAIN AND PERSONALITY. *Studies in the Psychological Aspects of Cerebral Neuropathology and the Neuropsychiatric Aspect of the Motility of Schizophrenics*

By Paul Schilder
Nervous and Mental Disease Publishing Co.
\$3.00 6×9 ; v + 136
Washington and New York

This series of lectures deals with problems of consciousness; problems of tonus; encephalitis; optic agnosia; speech disturbances; the postural model of the body; psychic and organic apparatus; actual causes and regression in neurosis and psychosis; transference in schizophrenia; impulse, postural and righting reflexes in relation to hyperkinetic states; akinetic states, stupor and negativism; mannerisms and emotions; catalepsy, motor troubles and personality. The author finds that organic lesions as well as psychic disturbances produce a regression to more primitive levels of behavior. The following bit of Lamarckianism amused us:

"We wish to mechanize what once had a real meaning. In that way, by the way, we can understand the genesis of organs of the organism. The organism produces tools in order not to be compelled again and again to a psychic effort."



THE ISLAND OF PENGUINS

By Cherry Kearton

Robert M. McBride and Co.

\$3.00 5½ x 8½; 248 New York

Because the book contains so much that is interesting in its text and particularly its numerous and excellent photographs the reader is the more irritated by its defects. These are of two sorts: First, a vagueness and lack of precision regarding simple points which finally make one dubious about the trustworthiness of anything in the book; and, second, the persistent attribution to the penguins of the same psychological motives, feelings and emotions that are in human beings associated with behavior objectively more or less like that observed among the penguins. Illustrative of the first point is the failure of the author to reveal the name or location of the island upon which he made his observations. It is vaguely said to be a small island with a lighthouse on it somewhere northwest of Capetown. As to the length of time Mr. Kearton stayed there the reader may take his choice among "many months" "several weeks," and "five months." On the second point it is obviously not only permissible but interesting and desirable to point out all possible objective similarities between the behavior of penguins and of men, but talk about she-penguins being "drowsily meditating on the perfect bliss of married life," or he-penguins "giving advice," or both of them being "house-proud," when it is continued for page after page throughout the book is not only unwarranted but finally becomes nauseating.

Altogether it is a pity that the author made such poor use of a remarkable opportunity. The illustrations, as has been said, are mainly excellent. They are the chief recommendation of the book, which lacks an index.



WHOLE AND PART METHODS IN TRIAL AND ERROR LEARNING. *Comparative Psychology Monographs*, Vol. 7, No. 5, Serial No. 35.

By Ella May Hanawalt

The Johns Hopkins Press

\$1.25 6½ x 10; 65 (paper) Baltimore

In the introduction to this paper the author gives an historical review of the work done on evaluating the experimental methods in the psychology of learning. She sums up the advantages and objections of the whole method and the part method which have been suggested or indicated by various investigators. A review of the experiments by Pechstein on white rats is given. The present study developed out of this line of work. The investigations were done in the psychological laboratories at the University of Michigan. The maze was the type designated as the "Shepard universal type." Fifteen male albino rats were used.

"The whole method proved to be superior to either the pure part, progressive part, reversed repetitive part, modified reversed repetitive part, or direct repetitive part methods for rats in learning maze patterns.

"Practice on parts and on part combinations before running the whole contributed to learning, but did not save enough to compensate for the extra energy required.

"Some important factors in causing waste in part learning were

- "a. Breaking up the unity of the total pattern.
- "b. Increasing the number of separate learning acts.
- "c. Learning in a direction opposite to that in which the learning must ultimately function.

"Compatibility of parts learned as parts when required to function with other parts or with the whole

was not immediate, but required practice of the part in its new relationship.

"Trained learners did not acquire increasing facility in learning problems of similar type and of comparable difficulty. They had attained a considerable uniformity of performance.

"The mastery of one part did not affect either positively or negatively the mastery of others when the problems were unique in character.

"The influence of distribution of repetitions on amount of energy required for learning for immediate recall is in need of further experimental study.

"Individual differences among learners is a probable factor in learning efficiency regardless of method employed."

Included in the paper are tables and figures. There is a bibliography of 31 titles.



YOUR COMPLETE LIFE

By Walter J. Banks

The Christopher Publishing House

\$1.25

5 $\frac{1}{4}$ x 7 $\frac{3}{4}$; 74

Boston

"For many years it has been my deep conviction that the principles of psychology should be expressed by someone in such simple language that anyone may interpret and apply their meaning to the various periods of development in life."

We cannot say that the result of this conviction, as expressed in the book before us, has seemed of great importance.



CONDITIONED EYELID REACTIONS TO A LIGHT STIMULUS BASED ON THE REFLEX WINK TO SOUNDS. *Psychological Monographs, Vol. XLI, No. 1, Whole No. 184.*

By Ernest R. Hilgard

Psychological Review Co.

75 cents Princeton, N. J., and Albany, N. Y.

6 $\frac{3}{4}$ x 9 $\frac{3}{4}$; v + 50 (paper)

An interesting paper, not easily reviewed within a limited space. The investigator selected the eyelid reaction because

"it involves a very light and mobile bodily member lending itself to a study of the controls which operate in the intact individual affecting relatively simple muscular activity. Involuntary blinking occurs more or less throughout the waking hours, and there is some measure of deliberate or voluntary control over the eyelid in opening or closing the eye. This interplay of reflex and voluntary action points to a probable significance of the eyelid reaction in an experimental program dealing with the modifiability of human behavior."

"Conditioned eyelid reactions were obtained from five out of eight subjects after successive presentations of a light stimulus preceding a sound stimulus by 2000 to 4000. The Dodge pendulum-photochronograph was used as the basic instrument for presenting the stimuli and for recording the stimuli and reactions photographically. . . . The light stimulus evoked at the start only occasional minimal unconditioned reflexes of a latency lower than that of the conditioned responses which later developed. The conditioned reaction appeared during the series of paired light and sound presentations as the initial component of a dual or dicrotic response, anticipatory to the second component which was the unconditioned reflex to sound. The isolated presentation of the light after such a series elicited a wink homologous with the first component of the dual response.

"The limited experimentation on conditioning as a learning process and the theoretical objections which may be raised against considering the conditioned reaction to be the unit of habit, suggest that for the present it may be better to think of conditioning as a sample of learning rather than as the foundation for learning theory."

Included in the paper are graphs and tables. There is a bibliography of 50 titles.



ANIMAL MOTIVATION. *Experimental Studies on The Albino Rat*

By C. J. Warden. *With the Collaboration of T. N. Jenkins, L. H. Warner, Marion Jenkins, E. L. Hamilton and H. W. Nissen*

Columbia University Press

\$5.00

5 $\frac{1}{2}$ x 8 $\frac{3}{4}$; xii + 302

New York

An account of studies on various drives—hunger, thirst, sex, maternal, and exploratory—in the albino rat, carried on by a uniform technique, the obstruction method. This consists essentially in

requiring the animal to undergo a disagreeable experience (in this case, an electric shock) in order to reach a desired object—food, water, etc. The volume is an important contribution to comparative psychology.



THE MEANING OF PSYCHOANALYSIS

By Martin W. Peck

Alfred A. Knopf, Inc.

\$2.50 5 x 7½; xix + 273 New York
AMERICAN TYPES. *A Preface to Analytic Psychology*

By James Oppenheim Alfred A. Knopf, Inc.

\$2.50 5 x 7½; 210 New York

These two books, by American disciples of Freud and Jung, are popular introductions to their subjects. Peck's book, based on lectures given in the Harvard Medical School, is distinctly the better written book. Oppenheim's attempt to expound Jung's psychology of types suffers, we feel, from a style unsuited to a reasoned scientific discussion. We cannot say that either book has brought us measurably nearer a complete acceptance of either theory.



DE OMNIBUS REBUS ET QUIBUSDEM ALIIS

A PRAGMATIST THEORY OF TRUTH AND REALITY

By Samuel S. S. Browne

Princeton University Press

\$2.00 6 x 9; 95 Princeton

We suggest that the following passage be read aloud:

The important point to understand is that A's being B does not imply that A has inhering in it a universal quality called B or B-ness. A can be B when it is not known, but B cannot be B when it is not known, for B is a universal constructed by

thought. B cannot be at all except in the knower's mind. Nevertheless, A can be B previous to its being known, for it is not necessary that B shall have become B in order that A shall become B. A's becoming B is ontological, but B's becoming B is epistemological. When A became B, an historical event occurred on which depends the applicability of B, when conceived, to A. This may be otherwise expressed by saying that particulars exist independently of thought, but universals do not. B is a universal, although there may be but one object in the Universe to which it can be applied. We cannot deny that A was B apart from thought if this denial is understood to mean that A was C instead of B, but we must deny it in the sense that B subsisted *qua* a universal inhering in A. If A-in-itself were really C, then C would be a universal and would have to be known; and having thus spoiled the truth of the conception that A is B, which we are not allowed to do *ex hypothesi*, we would be left with the same problem as before. Hence, A was not C; it was B; but it did not have B inhering in it as a quality. A's being B implies simply that when I conceive A, I conceive it to be B, and my conception is true.

"Of course, since the B-ness of A is my conception, so also is the A-ness of A. For A, although in one sense a particular existent independent of me, is also, in another sense, a universal conceived by me and hence having no being beyond my thought. In recognizing A as A, I am subsuming the particular A under the universal A. I am making A an epistemologically. It is not A until I have done so. It may be a chaos, but more probably it is not an *it* at all.

"Consequently we have no right to say that A is A wholly apart from thought, although we are justified in saying that it was A temporally previous to thought. This temporal previousness is itself part of my conception."



REASON AND NATURE. *An Essay on the Meaning of Scientific Method.*

By Morris R. Cohen

Harcourt, Brace and Co.

\$5.00 6 x 9; xxiv + 470 New York

A work which has taken Professor Cohen twenty years to write cannot profitably be reviewed in half a dozen lines. We can, however, heartily recommend our readers to try it for themselves, assuring them that they will find both pleasure and profit in it.

Professor Cohen has assisted the reviewer in the following paragraphs from his preface:

"To readers who have a predilection for conventional labels, I offer the following:

"I am a rationalist in believing that reason is a genuine and significant phase of nature; but I am an irrationalist in insisting that nature contains more than reason. I am a mystic in holding that all words point to a realm of being deeper and wider than the words themselves. But I reject as vicious obscuratism all efforts to describe the indescribable. I reject the euthanasia or suicide of thought involved in all monisms which identify the whole totality of things with matter, mind, or any other element in it. But I also reject the common dualism which conceives *the* mind and *the* external world as confronting each other like two mutually exclusive spatial bodies. I believe in the Aristotelian distinction between matter and form. But I am willing to be called a materialist if that means one who disbelieves in disembodied spirits; and I should refer to spiritists who localize disembodied spirits in space as cryptomaterialists. However, I should also call myself an idealist, not in the perverse modern sense which applies that term to nominalists like Berkeley who reject real ideas, but in the Platonic sense according to which ideas, ideals, or abstract universals are the conditions of real existence, and not mere fictions of the human mind.

"To those who labour under the necessity of passing judgment on this book in terms of current values, I suggest the following:

"The author seems out of touch with everything modern and useful, and yet makes no whole-hearted plea for the old. He believes in chance and spontaneity in physics and law and mechanism in life. He has no respect for *experience, induction, the dynamic, evolution, progress, behaviorism, and psychoanalysis*, and does not line up with either the orthodox or revolutionary party in politics, morals, or religion, though he writes on these themes. He offers no practical message to the man engaged in the affairs of life, and seems to be satisfied with purely contemplative surveys of existence."

THE HISTORY OF SCIENCE AND THE NEW HUMANISM

George Sarton

Henry Holt and Co.

1930

5 x 7 3/8; 178

New York

The New Humanism praised by Sarton in this book is a very different kind of

humanism from that which created quite a stir a couple of years ago. Sarton's humanism is to be built around science, but is to include much more.

The New Humanism will not exclude science but on the contrary exploit it to the utmost; it will minimize the danger of scientific knowledge abandoned to its own technicalities; it will extol the human implications of science, and reintegrate it into life; it will bring together into a single communion scientists, philosophers, artists and saints. It will confirm the oneness of mankind, not only in its achievements but in its aspirations. The evils of the so-called "machine age" have been caused by the aloofness of the old humanists as well as by the narrowmindedness of some scientists, but above all by the insatiable greed of men of prey. This "machine age" must go, and be replaced at last by the "scientific age;" we must prepare a new culture, the first to be deliberately based upon science, upon humanized science,—the New Humanism.

We can recommend the book unservedly to the attention of our readers.



SIR D'ARCY POWER: *Selected Writings*
1877-1930.

Oxford University Press

\$9.50 5 1/2 x 9; x + 368 New York

This is a delightful collection of historical essays by a distinguished British surgeon and historian of medicine. While mainly upon medical and surgical topics, the biologist will find much to interest him. It appears that Samuel Pepys' eye trouble, which caused him to give up his shorthand diary, would probably have been completely relieved by spectacles of the following prescription

+ 2 D. c. + 0.50 D. cyl. axis 90°

but nothing could be done for him in his day because nobody knew anything about astigmatism.

There is a good deal of interesting matter in this volume about John Hunter, William Harvey, and various other lesser lights. At the end is a short-title bibli-

ography of D'Arcy Power's writings to date. It includes 609 titles. There is an excellent index.



THE LOGIC OF SCIENCE

By Harold R. Smart

D. Appleton and Co.

\$2.50 $5\frac{1}{4} \times 8$; vii + 237 New York

A discussion of the nature of science and the logical and philosophical problems involved. On the whole, the discussion of mathematics and physics seems to us somewhat better done and more valuable than the discussion of the biological sciences.



FOUNDATIONS OF SCIENCE

By Garfield A. Bowden

P. Blakiston's Son and Co., Inc.

\$1.68 $5\frac{1}{4} \times 7\frac{1}{2}$; x + 753 Philadelphia

This textbook of general science for junior high schools is more interestingly written than most of its class.

SCIENCE AND FIRST PRINCIPLES.

By F. S. C. Northrop *The Macmillan Co.*

\$3.00 $5\frac{3}{4} \times 8\frac{1}{2}$; xiv + 299 New York

We refuse to express an opinion as to the merits of the cosmological theory offered in this book. That may be left to experts. The discussion of physical principles and the author's account of the history of science are well worth reading for their own sake.



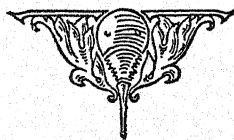
NOVIUS ORGANUM. *Essays in a New Metaphysic*

By James C. McKerrow

Longmans Green and Co.

\$3.00 $5\frac{1}{2} \times 7\frac{3}{4}$; viii + 277 New York

A collection of papers attempting to answer various philosophical, biological, economic, and moral questions. Some of the author's speculations are entertaining, but we have found most of them hardly convincing.





THE COST OF BIOLOGICAL BOOKS IN 1931

By JOHN R. MINER

Department of Biology, School of Hygiene and Public Health, Johns Hopkins University

IN ACCORDANCE with the usual custom of THE QUARTERLY REVIEW OF BIOLOGY, the present paper reports on the cost of the books which have been received during 1931. The books are classified by origin in the same rubrics as in previous reports.

The total number of pages reviewed in 1931 is 121,179, an increase of 8.9 per cent over 1930 and of 46.8 per cent over 1926. As in every previous year except 1928 the English-American books are the most expensive. However, these prices include both transportation and the United States tariff, whereas the prices for other groups, being for the country of publication, do not include either of these charges.

German books, which in every previous year had shown an increase in cost, in 1931 declined 3.8 per cent from 1930. They are still, however, well above the cost of any other group except the English-American.

Books published in the United States show a general downward trend in cost over the six years and are now 6.3 per cent below 1926. As these are the books

TABLE 1
Prices of biological books, 1931

ORIGIN	TOTAL PAGES	TOTAL COST	PRICE REP PAGE
			<i>cents</i>
English-American.....	8,516	\$193.30	2.27
German.....	10,323	180.26	1.75
Other Countries.....	1,970	30.11	1.53
England.....	2,742	32.68	1.19
United States.....	85,682	898.59	1.05
British Government....	366	3.76	1.03
France.....	8,148	55.96	0.69
U. S. Government.....	3,432	9.51	0.28

most used by American biologists, this is an auspicious phenomenon for the latter.

French books, which increased abruptly in price in 1928, have again in 1931 increased 46.8 per cent over 1930, so that

TABLE 2
Comparison of the prices of biological books from 1926 to 1931

ORIGIN	AVERAGE PRICE PER PAGE						CHANGE + OR - FROM 1930 TO 1931		CHANGE + OR - FROM 1926 TO 1931	
	1926	1927	1928	1929	1930	1931	Absolute	Relative	Absolute	Relative
	<i>cents</i>	<i>cents</i>	<i>cents</i>	<i>cents</i>	<i>cents</i>	<i>cents</i>	<i>cents</i>	<i>per cent</i>	<i>cents</i>	<i>per cent</i>
English-American.....	1.55	1.39	1.46	1.90	1.91	2.27	+0.36	+18.8	+0.72	+46.5
Other countries.....	1.51	0.78	1.13*	1.68	0.97	1.53	+0.56	+57.7	+0.02	+1.3
England.....	1.28	1.14	1.09	1.29	1.13	1.19	+0.06	+5.3	-0.09	-7.0
United States.....	1.12	1.09	1.14	1.14	1.09	1.05	-0.04	-3.7	-0.07	-6.3
Germany.....	1.09	1.20	1.48	1.65	1.82	1.75	-0.07	-3.8	+0.66	+60.6
British Government.....	—	0.96	1.26	0.39	1.19	1.03	-0.16	-13.4	+0.07†	+7.3†
France.....	0.35	0.36	0.45	0.47	0.47	0.69	+0.22	+46.8	+0.34	+97.1
U. S. Government.....	0.31	0.24	0.21	0.23	0.30	0.28	-0.02	-6.7	-0.03	-9.7

* With two special treatises omitted as explained in Vol. III, p. 601.

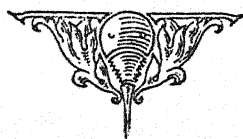
† Change from 1927 to 1931.

their price is now nearly double that of 1926. They are still, however, only about two-thirds as expensive as any other group of commercially produced scientific books. The biological books published by the United States Government are, as usual, at the bottom of the list.

Combining all books reviewed in 1931 the average price per page was 1.159 cents, an increase of 2.5 per cent as compared with 1930, and of 5.7 per cent as compared

with 1926. There has been no marked change in the general price level of the books reviewed.

It should be remembered that these reports are based on small samples of books in general and, for some countries, on small samples of the biological books published. The reader should, therefore, be mindful of the dangers of applying conclusions from samples to the general domain of book prices.



INDEX

- Abderhalden, E., Handbook of Biological Methods, 229, 238, 245, 246, 364, 371, 483
Acta Forestalia Fennica, 113
 Action potential, 59
 Alexander, C. P., Diptera of Patagonia and South Chile—Crane-Flies, 110
 Allee, W. C., Animal Aggregations, 468
 Allelocatalysis, 52
 ALLISON, F. E., Forms of Nitrogen Assimilated by Plants, 313-321
 All or nothing law, 62
 Almqvist, E., Great Biologists, 467
 Alvarez, W. C., Nervous Indigestion, 243
 Ammonia assimilation by plants, 316
 Antidromic conduction in nerves, 61
 Appleton, A. B., Laboratory Guide to Vertebrate Dissection, 114
 Application of power to flight, 86
 Arey, L. B., Developmental Anatomy, 242
 Arndt, H. J., *et al.*, Anatomy and Pathology of Spontaneous Diseases of Small Laboratory Animals, 484
 Artschwager, E., Dictionary of Biological Equivalents, 103
 Ash, E. C., The Practical Dog Book, 466

 Bachér, F., Saponification, 246
 Bacteria in nutrition of protozoa, 46
 Baerg, W. J., Birds of Arkansas, 479
 Bagley, W. C., Education, Crime, and Social Progress, 472
 Bailey, V., Animal Life of Yellowstone National Park, 110
 Baitsell, G. A., Manual of Biology, 103
 Baldwin, J. M., *et al.*, History of Psychology in Autobiography, 249
 Baldwin, S. P., Bird Banding by Systematic Trapping, 478
 Banks, W. J., Your Complete Life, 490
 Barker, L. F., The Relations of Psychology to Medicine and the Recognition and Treatment of Commoner Affective Disorders, 375
 Barlow, P., Tables of Squares, etc., 247
 Barnes, H. E., The Story of Punishment, 231
 Barrows, H. R., College Biology, 228
 Basler, A., Walking, 371
 Bateson, W., Mendel's Principles of Heredity, 102
 Baur, E., Introduction to Genetics, 101
 Bell, W. B., Some Aspects of the Cancer Problem, 114
 Belling, J., The Use of the Microscope, 102
 Berthier, J., and Lauvernier, C., Tables of General History, 352
 Besredka, A., Anaphylactic Shock and the Principle of Desensitization, 370
 Immunity in Infectious Diseases, 115
 Bethe, A., *et al.*, Medical Observations at the 9th Olympic Games, 359
 Beyer, C. M., Children of Working Mothers in Philadelphia, 471
 Binet, L., The Spleen, 117
 Bingham, W. V., *et al.*, Biology in Human Affairs, 472
 BIOCHEMISTRY (book reviews), 117, 246, 371, 486
Biogenetische Grundgesetze, 199
 Biological effects of short radiations, 253
 organization, 143
 processes, quantitative relations in, 281
The Biology Student, 229
 BIOMETRY (book reviews), 118, 247, 374, 487
 Bird flight, 84
 Birds, orientation and homing of, 208
 Bland-Sutton, J., The Story of a Surgeon, 243
 Block of nerve impulse, 62
 Bocker, C. C., *Silva Fennica*, 113
 Bodansky, M., Introduction to Physiological Chemistry, 117
 Bonar, J., Moral Sense, 249
 Books, biological, cost of, 494
 Bose, J. C., Life Movements in Plants, 483
 BOTANY (book reviews), 112, 238, 365, 482
 Bowden, G. A., Foundations of Science, 493
 Bower, F. O., Size and Form in Plants, 365
 Boyd, W., The Pathology of Internal Diseases, 485
 Brachet, A., The Egg and the Factors of Ontogenesis, 368
 Brambell, F. W. R., Development of Sex in Vertebrates, 247
 Brault, A., Glycogen, 485
 Braun, H., Metabolism of Bacteria, 245
 Breuil, H., and Burkitt, M. C., Rock Paintings of Southern Andalusia, 103
 Bridges, T. C., and Tiltman, H. H., Master Minds of Modern Science, 474
 Brieger, F., Self-sterility and Cross-sterility in Plants and Animals, 465
 Briffault, R., Rational Evolution, 349
 Britton, L., Hunger and Love, 475
 Brøgger, A. W., Ancient Emigrants, 235
 Bronson, W. S., Paddlewings, 480
 Brooks, C. H., Your Character from Your Handwriting, 357
 Broom, R., The Origin of the Human Skeleton, 367
 Brown, V. E., Hypermastigote Flagellates from the Termite Reticulitermes, 365
 Browne, C. R., Maori Witchery, 106

- Browne, S. S. S., A Pragmatist Theory of Truth and Reality, 491
- Bruce, D., and Reineke, L. H., Correlation Alinement Charts in Forest Research, 487
- Buchanan, E. D., and Buchanan, R. E., Bacteriology, 114
- Buchanan, R. E., and Fulmer, E. I., Physiology and Biochemistry of Bacteria, 112
- Buchholz, H. E., Fads and Fallacies in Present-day Education, 250
- Bühler, K., Mental Development of the Child, 250
- Burke, V., Revision of the Fishes of the Family Liparidae, 111
- Burks, B. S., Genetic Studies of Genius, 357
- Burt, W. H., Adaptive Modifications in the Woodpeckers, 349
- Butcher, E. O., 10
- Cajander, A. K., *Silva Fennica*, 113
- Camp, C. L., Study of the Phytosaurs, 223
- Campbell, E., General Elementary Botany, 241
- Cancer, treatment of, with vacuum tube oscillator, 324
- Cardan, J., The Book of My Life, 353
- Carnegie Institution of Washington, Contributions to Embryology, 241
- Papers from Tortugas Laboratory, 481
- Carter, W., Ecological Studies of the Beet Leaf Hopper, 479
- Castle, W. E., Genetics and Eugenics, 225
- Genetics of Domestic Rabbits, 224
- Cavazzi, F., The Glandular System and New Views in Medicine, 368
- One Can Rejuvenate, 369
- Chamberlain, C. J., Elements of Plant Science, 366
- Chapter of Child Health, 232
- Chatfield, C., and Adams, G., Proximate Composition of Fresh Vegetables, 372
- Chemical activation, radiation process of, 281
- changes in death, 173
- Child labor, 107
- Childe, V. G., The Bronze Age, 358
- Chinnery, E. W. P., Notes on the Natives of New Guinea, E Mira, St. Matthias, and New Britain, 360
- Chromosomal hypotheses of haploidy, 412
- Clark, A. H., The New Evolution: Zoögenesis, 99
- Coagulation and death, 172
- Coccidae in relation to haploidy, 423
- Cohen, M. R., Reason and Nature, 491
- Cohen-Kysper, A., The Determination Problem, 101
- Coker, R. E., Studies of Common Fishes of the Mississippi River at Keokuk, 110
- Cole, F. J., Early Theories of Sexual Generation, 373
- Collins, B. J., The Confused Nomenclature of Nycteribia and Spinturnix, 480
- Color vision in fishes, 329
- Comstock, J. H., *et al.*, A Manual for the Study of Insects, 479
- Concept of organism, 178
- Connell, F. H., The Morphology and Life Cycle of *Oxymonas Dimorpha*, 365
- Contributions to Marine Biology, 229
- Copeia*, 365
- Cost of biological books, 494
- Coudray, G., Contribution to the Study of Gram's Stain, 366
- Coulter, J. M., Barnes, C. R., and Cowles, H. C., Textbook of Botany, 114
- Cowles, R. P., A Biological Study of the Offshore Waters of Chesapeake Bay, 466
- Cowperthwaite, M. H., 19
- Crabb, E. D., Principles of Functional Anatomy of the Rabbit, 368
- Criteria of haploidy, 415
- Cuny, L., The Concentration of Bile Salts in the Bile and the Duodenal Liquid, 485
- Curti, M. W., Child Psychology, 376
- Daniel, J. F., Features in the Development of Ammocoetes, 485
- and Bennett, L. H., Veins in the Roof of the Buccopharyngeal Cavity of *Squalus sucklii*, 485
- Darmois, G., *et al.*, Lectures Given at the Laboratory of Microbiology of the Faculty of Pharmacy of Nancy, 367
- Dashiell, J. F., Direction Orientation in Maze Running by the White Rat, 119
- Davenport, C. B., 25
- Dearden, H., The Mind of the Murderer, 375
- Death and its causes, 167
- Dederding, D., Mb. Menière, 245
- Demuth, F., Tissue Culture Technique, 111
- DE OMNIBUS REBUS ET QUIBUSDEM ALIIS (book reviews), 121, 250, 377, 491
- Descamps, P., Social Status of Savage Peoples, 106
- Determinable, 180
- Developmental difference, 183
- route, 189
- Dodge, R., Conditions and Consequences of Human Variability, 374
- Drachman, J. M., Studies in the Literature of Natural Science, 251
- Dramas of French Crime, 109
- Draper, G., Disease and the Man, 358
- Driesch, H., 187, 202
- Dublin, L. I., and Vane, R. J., Causes of Death by Occupation, 104
- Dunn, E. R., Salamanders of the Family Plethodontidae, 235
- DuPuy, W. A., Our Plant Friends and Foes, 239
- Dürken, B., 197

- Eddy, J. W., Hunting the Alaska Brown Bear, 236
 Ellis, M. M., *et al.*, The Blood of North American Fresh-water Mussels, 477
 Elmer, W. P., and Rose, W. D., Physical Diagnosis, 234
 Elton, C., Animal Ecology and Evolution, 223
 Eltringham, H., Histological and Illustrative Methods for Entomologists, 237
 Embryology and genetics, relation between, 178
 Emerson, W. R. P., The Diagnosis of Health, 106
 Emich, F., Microchemical Handbook, 372
 Energy and ionic exchanges in physiological stimulation, 199
 Entropy, 146
Erkenntnis, 484
 Essig, E. O., A History of Entomology, 476
Euploes taylori, 53
 EVOLUTION (book reviews), 99, 223, 349, 464
 Extra-reflex effects, 76
 Fairchild, D., Exploring for Plants, 239
 Fearing, F., Reflex Action, 115
 Firker, J., 7
 Fischer, A., and Laser, H., Tissue Culture, 229
 Fishbein, M., Doctors and Specialists, 378
 Fisher, R. A., The Genetical Theory of Natural Selection, 100
 Fishes, color vision in, 329
 Fitting, H., *et al.*, Strasburger's Text-book of Botany, 240
 Fitzpatrick, H. M., The Lower Fungi, 240
 Five Years in Fargo, 232
 Flapping flight, 89
 Flight of birds, 84
 Florence, G., Modern Therapeutics, 370
 Fogerty, E., Stammering, 250
 Fort, C., Lol, 377
 Freeman, H., An Elementary Treatise on Actuarial Mathematics, 488
 Fry, C. L., The U. S. Looks at Its Churches, 108
 Fuller, A. B., and Bole, B. P., Jr., Observations on Some Wyoming Birds, 111
 Fulton, J. F., Physiology, 244
 Furfey, P. H., The Growing Boy, 120
 Gábor, D., 218
 Gadow, H., Jorullo, 350
 Gager, L. T., Hypertension, 369
 Gann, T., and Thompson, J. E., The History of the Maya, 474
 Garrod, A. E., The Inborn Factors in Disease, 475
 Garth, T. R., Race Psychology, 376
 Gaskell, G. A., A New Theory of Heredity, 350
 Gellhorn, E., *et al.*, General Physiology, 486
 GENERAL BIOLOGY (book reviews), 102, 225, 350, 465
 Genetic difference, 183
 GENETICS (book reviews), 101, 224, 350, 465
 Genetics and embryology, relation between, 178
 Genevois, L., Metabolism and Functions of Cells, 371
 GERARD, R. W., Nerve Conduction in Relation to Nerve Structure, 59-83
 Germ cells, origin of, 1
 Gesell, A., The Guidance of Mental Growth in Infant and Child, 376
 Gini, C., *et al.*, Population, 234
 Ginzburg, B., The Adventure of Science, 377
 Gipsy-moth, intersexuality in, 125
 Gliding flight, 89
 GOLDSCHMIDT, RICHARD, Analysis of Intersexuality in the Gipsy-moth, 125-142
 Goldschmidt, R., Intersexuality, 466
 Goldsmith, J. B., 23
 Goodrich, E. S., Studies on the Structure and Development of Vertebrates, 241
 Granet, M., Chinese Civilization, 355
 Gray, H., Anatomy, 242
 Grimpe, G., and Wagler, E., Fauna of the North and Baltic Seas, 364
 Grinnell, J., *et al.*, Vertebrate Natural History of a Section of Northern California, 237
 Günther, H. F. R., *Rassenkunde* of the Jewish People, 235
 Gurwitsch, A., 215
 Gutsell, J. S., Natural History of the Bay Scallop, 478
 Guyénot, É., Heredity, 350
 Variation and Evolution, 223
 Guyer, M. F., Animal Micrology, 111
 Haemoglobin, oxidation and reduction of, 285
 Haempel, O., Fishery Biology of Alpine Lakes, 111
 Haldane, J. B. S., Enzymes, 246
 Hall, E. R., Critical Comments on Mammals from Utah, 482
 Hanawalt, E. M., Whole and Part Methods in Trial and Error Learning, 489
 Haploidy in Metazoa, 411
 Harding, T. S., Fads, Frauds and Physicians, 377
 Hargitt, G. T., 4
 Harris, J. A., *et al.*, The Measurement of Man, 234
 Harvey, R. B., Plant Physiological Chemistry, 240
 Heart beat in hibernation, 447
 Hegner, R. W., 13
 College Zoology, 481
 Laboratory Guide for College Zoology, 481
 Heidenhain, L., On the Problem of Malignant Tumors, 371
 Heinlein, J. H., Preferential Manipulation in Children, 119
 Henrici, A. T., Molds, Yeasts, and Actinomycetes, 238

- Henry, D. P., Species of Coccidia in Chickens and Quail in California, 481
Study of the Species of Eimeria Occurring in Swine, 365
- HEYS, FLORENCE, The Problem of the Origin of Germ Cells, 1-45
- Hibernation in mammals, 439
- Hickman, C. P., Laboratory Manual in College Physiology, 117
- Hierarchical order, 178
- Hildebrand, S. F., and Cable, L. E., Development and Life History of 14 Teleostean Fishes, 480
- Hilgard, E. R., Conditioned Eyelid Reactions to a Light Stimulus Based on the Reflex Wink to Sounds, 490
- Hill, A. V., Adventures in Biophysics, 485
- Hill, L., Philosophy of a Biologist, 352
- Hirsch, N. D. M., Twins, 230
- Histological difference, 185
- Hitchcock, E. A., A Traveler in Indian Territory, 356
- Hocking, W. E., Types of Philosophy, 122
- Hogben, L., The Nature of Living Matter, 226
Principles of Animal Biology, 228
- Holcomb, R. C., A Century with Norfolk Naval Hospital, 377
- HOLLAENDER, ALEXANDER, and SCHORFFEL, EUGENE, Mitogenetic Rays, 215-222
- Holt, E. B., Animal Drive and the Learning Process, 374
- Holzworth, J. M., The Wild Grizzlies of Alaska, 236
- Homing of Birds, 208
- Horsters, H. and H., Synthesis of Pyridine Compounds, 246
- Howard, L. O., History of Applied Entomology, 361
- Howell, W. H., Physiology 243
- Hrdlička, A., Children Who Run on All Fours, 360
- Hughes-Schrader, Sally, 411
- Hulbert, A. B., Soil, 233
- HUMAN BIOLOGY (book reviews), 103, 230, 352, 469
- Humphrey, R. R., 22
- Hunt, H. R., Some Biological Aspects of War, 359
- Huybrechts, M., pH and Its Measurement, 371
- Imms, A. D., Recent Advances in Entomology, 363
- Intersexuality in the gipsy-moth, 125
- Intuition, uses of, 165
- Irritability in hibernation, 448
- Jeans, J., The Mysterious Universe, 378
- Jennings, H. S., 204
The Biological Basis of Human Nature, 107
- Johnsen, A., The Difference between Minerals and Living Beings, 102
- Johnson, A. M., Taxonomy of the Flowering Plants, 482
- Johnson, C. S., The Negro in American Civilization, 230
- JOHNSON, GEORGE E., Hibernation in Mammals, 439-461
- Johnston, A., Life and Letters of Sir Harry Johnston, 110
- Jones, J. E., Some Familiar Wild Flowers, 484
- Jordan, H. E., Histology, 242
- Judy, W., Principles of Dog Breeding, 224
- Juvenile Delinquency in Maine, 108
- Kahn, M. C., Djuka: The Bush Negroes of Dutch Guiana, 471
- Kearton, C., The Island of Penguins, 489
- Keeler, C. E., The Laboratory Mouse, 350
- Kestner, O., *et al.*, The Problem of Life, 351
- Key action, 156
- Kilduffe, R. A., The Clinical Interpretation of Blood Examinations, 369
- King, W. P. (Ed.), Behaviorism: A Battle Line, 249
- Kingsley, N. H., and Menge, E. J., Laboratory Studies, Demonstrations, and Problems in Biology, 103
- Kirby, H., Trichomonad Flagellates from Termites, 481
- Klein, A., and Thomas, L. C., Posture and Physical Fitness, 470
- Kleinschmidt, O., The Formenkreis Theory and the Progress of the Organic World, 349
- Klenck, W., and Scheidt, W., Lower Saxon Peasants, 108
- Kofoed, C. A., and MacLennan, R. F., Ciliates from *Bos Indicus* Linn., 238
- Konikow, A. F., Physician's Manual of Birth Control, 373
- Kuppanyi, T., The Conquest of Life, 228
- Kostychev, S., Chemical Plant Physiology, 486
- Krafft, C. F., Spirazines, 246
- Krasusky, W. S., Constitutional Types of Children, 361
- Krober, A. L., and Waterman, T. T., Source Book in Anthropology, 475
- Kuczynski, R. R., Birth Registration and Birth Statistics in Canada, 357
- Kudo, R. R., Handbook of Protozoology, 363
- Lamb, F. W., Human Experimental Physiology, 244
- Laroche, G., *et al.*, Alimentary Anaphylaxis, 245
- Lartigue, A., General Biodynamics, 103
- Lasseur and Vernier, Work of the Laboratory of Microbiology of the Faculty of Pharmacy of Nancy, 366

- Latane, J. H., The History of the American People, 360
- Latent period, 259
- Leakey, L. S. B., *et al.*, The Stone Age Cultures of Kenya Colony, 469
- Lehmann, E., and Aichele, F., Physiology of Sprouting of Cereals, 483
- Leitch, J. L., Water Exchanges of Living Cells, 364
- LEPESCHKIN, W. W., Death and Its Causes, 167-177
- Leventis, C., Sex Glands Function and the Human Life, 372
- Leverett, F., Pleistocene of Northern Kentucky, 224
- Lhermitte, J., Sleep, 376
- Liddell, E. G. T., and Sherrington, C., Mammalian Physiology, 116
- Lindsey, A. W., The Problems of Evolution, 465
- Lovejoy, A. O., The Revolt against Dualism, 123
- LUCK, J. MURRAY, SHEETS, GRACE, and THOMAS, JOHN O., The Role of Bacteria in the Nutrition of Protozoa, 46-58
- Luckiesh, M., Artificial Sunlight, 245
- Luquet, G.-H., Art and Religion of Fossil Man, 107
- Lymantria dispar*, 125
- Lynch, J. E., and Noble, A. E., Notes on the Genus *Endosphaera* Engelmann, 365
- Macauley, F. R., The Smoothing of Time Series, 488
- MacBride, E. W., Evolution, 224
- MacCallum, W. G., William Stewart Halsted, 353
- MacDougal, D. T., The Green Leaf, 239
- McDougall, W. B., Plant Ecology, 366
- MacLennan, R. F., and Connell, F. H., The Morphology of Eupoterion Pernix, 482
- McGill, N. P., Child Labor in New Jersey, 354
- McKerrow, J. C., Novius Organum, 493
- McKINLEY, G. MURRAY, and McKINLEY, JOHN G., JR., The Vacuum Tube Oscillator in Biology, 322-328
- McMurrich, J. P., Leonardo da Vinci the Anatomist, 241
- Mammals, hibernation in, 439
- Mann, W. M., Wild Animals in and out of the Zoo, 109
- Manuel, H. T., The Education of Mexican and Spanish Speaking Children in Texas, 358
- Marie-Victorin, Frère, *Anacharis Canadensis*, 367
- The Genus *Rorippa* in Quebec, 367
- Laurentian Variations of *Populus tremuloides* and of *P. grandidentata*, 367
- Markwardt, L. J., Comparative Strength Properties of Woods Grown in the United States, 112
- Martin, P., Contribution to the Study of the Serologic Precipitation and Agglutination of Mushrooms, 367
- Martin, R., Observations on the Biology of Various Mushrooms, 366
- Matla, J. L. W. P., The Solution of the Mystery of Death, 102
- Matthews, E. N., Children in Fruit and Vegetable Canneries, 107
- Maximov, N. A., Textbook of Plant Physiology, 240
- Maximow, A. A., Histology, 242
- Maxwell's "Demon," 148
- Mead, M., Growing Up in New Guinea, 231
- Meek, A., The Progress of Life, 100
- Meier, W. H. D., and Meier, L., Essentials of Biology, 468
- Melders, K., *Commentationes Forestales*, 113
- Mendelism, 203
- Menge, E. J. v. K., A Survey of National Trends in Biology, 352
- Merrill, F. and M., Among the Nudists, 473
- Metazoa, haploidy in, 411
- Metcalf, Z. P., Text-Book of Economic Zoology, 111
- MBTZ, C. W., Unisexual Progenies and Sex Determination in *Sciara*, 306-312
- Metzger, H., Newton, Stahl, Boerhaave, and Chemical Doctrine, 117
- Michon, P., Blood Groups and Transfusion, 101
- Miklaszewski, J., *Commentationes Forestales*, 113
- Miller, E. C., Plant Physiology, 483
- MILLER, GERRIT, JR., The Primate Basis of Human Sexual Behavior, 379-410
- MINER, JOHN R., The Cost of Biological Books in 1931, 494-495
- Mitogenetic rays, 215
- Money-Kyrle, R., The Meaning of Sacrifice, 120
- Morgan, A. H., Field Book of Ponds and Streams, 102
- MORPHOLOGY (book reviews), 114, 241, 367, 484
- Mortality curve, three types of, 462
- Mudgett, B. D., Statistical Tables and Graphs, 487
- Muscle metabolism, quantum relations in, 292
- Mustard, H. S., Cross-sections of Rural Health Progress, 232
- Myelin, 69
- National Institute of Health Bulletin, 480
- Natural death, 176
- Naumann, E., Life of Lake Bottoms, 103
- Nelson, L. A., Variations in Development and Motor Control in Goiterous and Non-goiterous Adolescent Girls, 108
- Nerve conduction, 59
- impulse, quantum relations in conduction of, 289
- Neurofibrils, 65
- NEW BIOLOGICAL BOOKS, 99-123, 223-251, 349-378, 464-493
- Newton, Isaac, 251
- Nicholson, E. M., The Study of Birds, 238
- Niggli-Hürlimann, B., Anthropological Investigations in Kindergartens of Zurich, 476

- Ninth International Congress of Psychology: Proceedings and Papers, 121
- Nitrogen, forms of, assimilated by plants, 313
- Non-difference, 179
- Northrop, F. S. C., Science and First Principles, 493
- Nutrition of protozoa, 46
- Oberholser, H. C., A New Genus of African Starlings, 111
- Notes on a Collection of Birds from Arizona and New Mexico, 111
- Oppenheim, J., American Types, 491
- Organism, concept of, 178
- Organization, biological, 143
- Orientation of birds, 208
- Origin of germ cells, 1
- O'Roke, E. C., The Morphology, Transmission, and Life-history of *Haemoproteus lophortyx* O'Roke, 238
- Osborn, H. F., Cope: Master Naturalist, 464
- Fifty-two Years of Research, Observation and Publication, 232
- Our City—New York, 361
- Ovary, histology of, 30
- PACKARD, CHARLES, Biological Effects of Short Radiations, 253-280
- Paget, R., Human Speech, 119
- Parkes, A. S., 26
- Internal Secretions of the Ovary, 118
- Parkhurst, W., The Anatomy of Music, 109
- Parsons, T. R., The Materials of Life, 117
- Parthenogenesis, 431
- Pearl, R., Introduction to Medical Biometry and Statistics, 118
- Pearson, H. H. W., Gnetales, 113
- Peck, M. W., The Meaning of Psychoanalysis, 491
- Photosynthesis in plants, 283
- Physicians Hospital of Plattsburgh, Medical and Surgical Yearbook, 116
- PHYSIOLOGY AND PATHOLOGY (book reviews), 114, 243, 368, 485
- Pickett-Thomson Research Laboratory, Annals of, 371
- Pighini, G., Journeys and Scientific Excursions of Spallanzani, 251
- Pigment cells in fishes, 342
- Pitkin, W. B., The Psychology of Achievement, 359
- Piza, S. de T., Jr., Localization of Factors in the Linin, 225
- Place, F., Illustrations and Proofs of the Principles of Population, 233
- de Pomerai, R., Marriage, 373
- Popenoe, P., Practical Applications of Heredity, 125
- Power, D'A., Selected Writings, 492
- Power: weight ratio, 84
- Prenatal Care, 360
- Primate basis of human sexual behavior, 379
- Probability, meaning of, 144
- Promiscuity, 398
- Promotion of the Welfare and Hygiene of Maternity and Infancy, 476
- Protozoa, nutrition of, 46
- Przibram, H., Experimental Zoology, 237
- PSYCHOLOGY AND BEHAVIOR (Book reviews), 119, 247, 374, 488
- Quantitative relations in biological processes, 281
- Radcliffe, M. M., Health and Continual Youth, 373
- Radiation hypothesis of chemical activation, 281
- short, biological effects of, 253
- Rádl, E., History of Biological Theories, 228
- Ramsay, L. W., and Lawrence, C. H., Garden Pools, 468
- Rape, social influence of, 402
- Reboux, P., New French Cooking, 121
- Reduction division in haploids, 429
- Reed, H. D., and Young, B. P., Laboratory Studies in Zoology, 111
- Reflex arc, 72
- Refractory period of nerves, 61
- Regeneration and germ cell origin, 24, 29
- Reiser, O. L., Humanistic Logic for the Mind in Action, 248
- Reiter, T., 218
- Report on the Preparation of Fruit for Market, 367
- Respiration in hibernation, 446
- metabolism in plants, 283
- Retzlaff, E., and Kneip, J., The Physiognomy of Age, 476
- Reuter, E. B., Race Mixture, 355
- and Runner, J. R., The Family, 476
- Rhythmical processes, quantum relations among, 288
- Richards, A., 18
- Rigg, G. B., College Botany, 114
- Rignano, E., The Nature of Life, 227
- Rinne, F., Boundary Problems of Life, 469
- Robinson, C. H., Seventy Birth Control Clinics, 234
- Roddis, L. H., Edward Jenner, 244
- Rostand, J., The Formation of the Being, 225
- Russell, E. S., The Interpretation of Development and Heredity, 351
- Ruthven, A. G., A Naturalist in a University Museum, 468
- Sachar, A. L., History of the Jews, 106
- Saidla, L. E., and Gibbs, W. E., Science and the Scientific Mind, 378
- St. Hill, K., Hands and Faces, 105

- Saller, K., Anthropology, 361
 Saprophytic rearing of protozoa, 50, 56
 Sarton, G., The History of Science and the New Humanism, 492
 Saunders, A. R., Maize in South Africa, 482
 Saville, M. H., Tizoc, Great Lord of the Aztecs, 108
 Sayers, R. R., and Davenport, S. J., Review of Carbon Monoxide Poisoning, 116
 Saz, E., Customs of Insects, 238
 Scarborough, J. B., Numerical Mathematical Analysis, 374
 Scarth, G. W., and Lloyd, F. E., Elementary Course in General Physiology, 115
 Schilder, P., Brain and Personality, 488
 Schmidt, J., The Atlantic Cod and Local Races of the Same, 466
 Schoeffel, E., 215
 SCHRADER, FRANZ, and HUGHES-SCHRADER, SALLY, Haploidy in Metazoa, 411-438
Sciara, 306
 Scott, G. G., Laboratory Manual of General Biology, 103
 The Science of Biology, 103
 Sensitivity to radiation, 261
 Sex (book reviews), 118, 247, 372, 486
 Sex determination, 432
 in *Sciara*, 306
 Sex reversal, 134
 and germ cell origin, 7
 Sexual behavior, human, primate basis of, 379
 Sheets, Grace, 46
 Sheldon, C., The Wilderness of Denali, 236
 Shetrone, H. C., The Mound-builders, 235
 Shipley, M., The Key to Evolution, 100
 Shumway, W., Vertebrate Embryology, 114
 Siemens, H. W., Heredity, Race Hygiene, and Population Policy, 105
Silva Fennica, 113
 Simkins, C. S., 8
 Simon, A. L., The Art of Good Living, 378
 Skalet, M., The Significance of Delayed Reactions in Young Children, 376
 Slosson, E. E., Short Talks on Science, 122
 Smallwood, W. M., Text-book of Biology, 103
 Smart, H. R., The Logic of Science, 493
 Smith, J. J., Social Psychology, 250
 Smith, K. M., A Textbook of Agricultural Entomology, 477
 Smock, J. C., The Greek Element in English Words, 378
 SNYDER, CHARLES D., Quantitative Relations in Biological Processes and the Radiation Hypothesis of Chemical Activation, 281-305
 Snyder, H., Bread, 116
 Soares, J. C. de M., Rubber, 366
 Soaring flight, 93
 Southwell, T., Fauna of British India—Cestoda, 110, 364
 Specializations in flight, 87
 Specific difference, 179
 Spiegel-Adolf, M., The Globulines, 117
 Stahl, F. A., Concerning Earliest First Growth in the Human Ovum, etc., 484
 Stedman, T. L., Practical Medical Dictionary, 122
 Steffensen, J. F., Some Recent Researches in the Theory of Statistics and Actuarial Science, 488
 Stephenson, J., The Oligochaeta, 109
 Sterilization of protozoa, 48
 Stibbe, E. P., Introduction to Physical Anthropology, 361
 Stiles, C. W., and Nolan, M. O., Key Catalogue of Parasites Reported for Bats, 480
 Stimulation by radiation, 264
 Stockard, C. R., The Physical Basis of Personality, 470
 Stopford, J. S. B., Sensation and the Sensory Pathway, 117
 Strong, R. P., Liberia and the Belgian Congo, 237
 Swezy, O., 20
 Swift, C. H., 14
 Swingle, W. W., 17
 Synapse, physiological mechanisms of, 74
 Synthetic fevers, 325
 SZÁBÓ, ISTVÁN, The Three Types of Mortality Curve, 462-463
 Tähtinen, O., *Silva Fennica*, 113
 Taxonomic difference, 185
 Taylor, H. C., Outlines of Agricultural Economics, 474
 Temperature in hibernation, 444
 Terroine, E. F., and Janot, M. M., Biology (Numerical Data), 371
 Thermic effects of death, 174
 Thierfelder, H., and Klenk, E., Chemistry of Cerebrosides and Phosphatides, 117
 Thomas, John O., 46
 Thomas, P., Comparative Study of *Bacillus mesentericus fuscus* Flügge and of *Bacillus mesentericus niger* Lunt, 366
 Thomas, S., Bacteriology, 113
 Thompson, J. T., 18
 Thornton, H. R., Among the Eskimos of Wales, Alaska, 475
 Thought and organization, 162
 Tiffany, L. H., The Oedogoniaceae, 113
 Titchener, E. B., Systematic Psychology: Prolegomena, 120
 Tobey, J. A., Riders of the Plagues, 370

- Topley, W. W. C., and Wilson, G. S., Principles of Bacteriology and Immunity, 112
- Townsend, C. H., The Fur Seal of the California Islands, 363
- Troland, L. T., Psychophysiology, 247
- Turnbull, H. W., The Great Mathematicians, 118
- Unisexual progenies in *Sciara*, 306
- Vacuum tube oscillator in biology, 322
- Vallery-Radot, P., and Heimann, V., Specific Hypersensitiveness in Cutaneous Affections, 370
- and Rouquès, L., The Phenomena of Shock in Urticaria, 368
- Van Cleave, H. J., Linville, H. R., and Kelley, H. A., Biological Principles in General Zoology, 111
- Vandel, A., Parthenogenesis, 363
- Van de Velde, Th. H., Ideal Marriage, 486
- Vanneman, A. S., 15
- Verne, J., Colors and Pigments of Living Beings, 229
- Vignon, P., Introduction to Experimental Biology, 225
- Villaret, M., Peripheral Venous Pressure, 485
- Vines, S. H., The Proteases of Plants, 113
- Voisin, G., French Cooking for All, 121
- Volterra, V., Lessons on the Mathematical Theory of the Struggle for Existence, 374
- Walter, H. E., Genetics, 101
- Warden, C. J., *et al.*, Animal Motivation, 490
- Warner, E. F., and Smith, G., Children of the Covered Wagon, 232
- WARNER, LUCIEN H., Facts and Theories of Bird Flight, 84-98
- Orientation and Homing of Birds, 208-214
- The Problem of Color Vision in Fishes, 329-348
- Warthin, A. S., The Creed of a Biologist, 227
- Old Age, 229
- Waterman, H. C., Evolution of the Pelvis of Man and Other Primates, 101
- WATSON, DAVID L., Biological Organization, 143-166
- Watson, J. B., Behaviorism, 250
- Weinert, H., Paleolithic Man, 235
- Weismann, A., 1, 190
- Weiss, H. B., and Ziegler, G. M., Thomas Say, 362
- Weiss, P., Physiology of Development, 364
- Weissenberg, R., Human Embryology, 242
- Weymouth, F. W., and McMillin, H. C., Relative Growth and Mortality of the Pacific Razor Clam, 480
- Wheeler, R. H., Readings in Psychology, 121
- Wheeler, W. M., Demons of the Dust, 362
- Wiebe, A. H., Plankton Production in Fish Ponds, 238
- Wieman, H. L., Introduction to Vertebrate Embryology, 114
- Willey, A., Lectures on Darwinism, 465
- Winston, S., Illiteracy in the United States, 474
- Wissler, C., Growth of Children in Hawaii, 354
- Wolbarst, A. L., Generations of Adam, 118
- Wolvekamp, H. P., Invertebrate Metabolism, 245
- Woodward, J. H., The "Concept of Organism" and the Relation between Embryology and Genetics, 178-207
- Woodruff, L. L., Foundations of Biology, 103
- Woods, H. M., and Russell, W. T., An Introduction to Medical Statistics, 487
- Wyatt, B. L., Chronic Arthritis and Rheumatoid Affections, 370
- Yonge, C. M., A Year on the Great Barrier Reef, 467
- Young, K., Social Psychology, 248
- Zand, N., The Choroid Plexuses, 114
- Zoology (book reviews), 109, 235, 361, 476

